Journal of Theoretical Biology 424 (2017) 11–25

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtbi

A necessary condition for dispersal driven growth of populations with discrete patch dynamics☆

Chris Guiver[a,*], David Packman[b], Stuart Townley[b]

[a] Department of Mathematical Sciences, University of Bath, Bath, UK
[b] Environment and Sustainability Institute, College of Engineering Mathematics and Physical Sciences, University of Exeter, Penryn Campus, Cornwall, UK

ARTICLE INFO

Article history:
Received 28 November 2016
Revised 6 March 2017
Accepted 8 March 2017
Available online 18 April 2017

Keywords:
Common linear Lyapunov function
Dispersal driven growth
Patch dynamics
Positive dynamical system
Population ecology
Population persistence

ABSTRACT

We revisit the question of when can dispersal-induced coupling between discrete sink populations cause overall population growth? Such a phenomenon is called dispersal driven growth and provides a simple explanation of how dispersal can allow populations to persist across discrete, spatially heterogeneous, environments even when individual patches are adverse or unfavourable. For two classes of mathematical models, one linear and one non-linear, we provide necessary conditions for dispersal driven growth in terms of the non-existence of a common linear Lyapunov function, which we describe. Our approach draws heavily upon the underlying positive dynamical systems structure. Our results apply to both discrete- and continuous-time models. The theory is illustrated with examples and both biological and mathematical conclusions are drawn.

1. Introduction

Persistence is a fundamental line of enquiry in the mathematical modelling of populations. Models for populations date back as early as the work of Leonardo of Pisa in the 1200s, with later notable historical contributions by Malthus in the 1790s, Verhulst in the 1840s and Lotka and Volterra in the 1920s, see Murray (2002). More recently persistence, as a property of mathematical models, has been incorporated into mainstream mathematical biology with detailed treatments from both deterministic (Smith and Thieme, 2011) and stochastic (Schreiber, 2012) perspectives. There are obvious applications of a theoretical framework which describes and explains persistence, from ecosystem composition and function, natural resource management or conservation, to the control of invasive or pest species.

A simple class of linear models for populations assumes a discrete-time unit, and partitions the population according to some discrete age-, stage- or size-class, which leads to the linear vector difference equation

$$x(t+1) = Ax(t), \quad x(0) = x^0, \quad t \in \mathbb{N}_0, \tag{1.1}$$

called a matrix population projection matrix model. The reader is referred to, for example, the monograph of Caswell (2001) for a thorough treatment of matrix population models. The matrix A in (1.1) models vital rates or life-history parameters of the population and the vector $x(t)$ denotes the abundances of each stage-class at time-step t, with initial stage-structure determined by x^0. Simple linear algebra can be used to project structured populations through time and, under biologically reasonable mathematical assumptions, the long-term or asymptotic behaviour of the solution x of (1.1) is determined by the spectral radius of A, denoted $r(A)$, which is also an eigenvalue of A. Correspondingly, this term is often called the *asymptotic growth rate*, the *dominant eigenvalue* or sometimes just λ. The situations $r(A) < 1$ or $r(A) > 1$ have been termed a (deterministic) sink or source population as they correspond to the model predicting asymptotic extinction or growth, respectively.

The model (1.1) does not include an explicit spatial component which is an obvious limitation since in reality all populations exhibit a spatial extent and range. Spatial structure is known to be a crucial factor affecting the persistence of metapopulations, identified in the seminal work of Pulliam (1988). Patch dynamics is a term used to describe the situation whereby a population's temporal dynamics are augmented with a (finite) discrete-spatial structure, that is, finitely many distinct locations or patches. A patch model is obtained from (1.1) by, in essence, connecting multiple copies of (1.1) together via dispersal. One explanation for persistence of sink populations, either individually or with a patch

☆ This work was supported by EPSRC research grant EP/I019456/1.
* Corresponding author.
E-mail addresses: c.guiver@bath.ac.uk, c.w.guiver@gmail.com (C. Guiver), dsp204@ex.ac.uk (D. Packman), s.b.townley@ex.ac.uk (S. Townley).

http://dx.doi.org/10.1016/j.jtbi.2017.03.030
0022-5193/

structure, is the contribution from external immigration. Amongst a variety of possible references, we refer the reader to, for example, Gonzalez and Holt (2002), Holt et al. (2003) and Roy et al. (2005) as well as Matthews and Gonzalez (2007) or Eager et al. (2014a) which, broadly, have explored and estimated both theoretically and empirically the effects of immigration on population abundance and distribution. It is certainly the case, by definition, that models for any number of deterministic sinks in the absence of dispersal or immigration predict asymptotic decline. However, perhaps somewhat counter-intuitively, deterministic sinks, when coupled by dispersal, may lead to a population that persists asymptotically, understood appropriately; a phenomenon known as dispersal driven growth (DDG). DDG may occur in the *absence* of immigration or a (single) deterministic source patch.

For sink patches in isolation, zero is a stable equilibrium. Moreover, dispersal is a diffusive and not (directly) creative process — indeed, there may be a mortality risk associated with dispersing — and so appears an *a priori* stabilising process. At first glance, therefore, DDG posits that a seemingly stabilising connection of stable objects need not be stable. Such dynamical behaviour should not come as surprising, however, as “instability from stability” occurs elsewhere in mathematical biology; the most famous and now archetypal example being proposed by Turing (1952) as a mechanism for the formation of spatial heterogeneity from a homogeneous steady state in reaction-diffusion equations. The instability that arises in reaction-diffusion equations caused by diffusion, which is usually ‘stabilising’ (in the sense that heat dissipates over time), now bears his namesake Turing Instability and is also known as Diffusion Driven Instability; see, for example, Murray (1982).

The recent paper (Elragig and Townley, 2012) presents a necessary condition for Turing Instability in terms of the non-existence of a so-called joint or common Lyapunov function, and builds on Neubert et al. (2002). To summarise Elragig and Townley (2012), when the linearized reaction matrix and the diffusion matrix admit a common Lyapunov function, Turing Instability is not possible. Common Lyapunov functions are a powerful tool which have primarily been considered in systems & control theory (Hinrichsen and Pritchard, 2005; Sontag, 1998) as a tool for understanding the stability (or otherwise) of switched systems — typically difference or differential equations which are governed by multiple distinct operating modes. We refer the reader to, for example, Liberzon and Morse (1999) or Lin and Antsaklis (2009) and the references therein, for further background on switched systems and common Lyapunov functions.

Here we present a necessary condition for DDG for two classes of deterministic discrete-time (difference equation) models of populations with a discrete-patch spatial structure. To summarise our results briefly, when the patch dynamics (which are governed by a set of matrices in the linear case) admit a certain common Lyapunov function, then DDG is not possible for any dispersal structure or parameters and consequently, the model predicts asymptotic decline of the population to extinction. The motivation for our study is that, we posit, describing analytically the onset of DDG as a function of the model parameters is often intractable — although in the sequel we suggest how perturbation tools from robust control theory may play a role. When the dynamics on each patch are assumed to be governed by a linear model (of the form (1.1) when no dispersal is present); testing for DDG amounts to computing eigenvalues of the dispersal-coupled system which is numerically straightforward, at least for low-dimensional problems. However, such an approach does not provide much insight into the relationships between patch dynamics and structure, dispersal and the onset of DDG. Moreover, computing eigenvalues for large problems may be often computationally intensive, especially to fully traverse all possible parameter values. The readily checkable “common Lyapunov function” test for DDG partially obviates the requirement for such calculations. Our approach follows the spirit of Elragig and Townley (2012), although we demonstrate that the notion of common quadratic stability used there is not the correct notion for testing for DDG. Instead a notion of common *linear* stability is required.

One motivation for the present line of enquiry is that the necessary condition for DDG to be possible imposes conditions on the life-histories of metapopulations. For example, DDG is not possible in models where the patch dynamics are sufficiently “similar” (as such sets of matrices admit a common linear Lyapunov function). Additionally, for the dispersal models we consider, DDG is only possible when at least one patch is “reactive”, meaning that certain stage-classes must exhibit short-term (transient) population growth (Ezard et al., 2010; Hastings, 2004; Stott et al., 2011).

Pertinent to models for dispersal, and underpinning our mathematical approach, is the fact that they are instances of positive dynamical systems — dynamical systems which leave a positive cone invariant. Possibly the most natural positive cone is the nonnegative orthant in real n-dimensional Euclidean space. Positive dynamical systems are well-studied objects, motivated by their prevalence in models arising in a diverse range of fields from biology, chemistry, ecology and economics to genetics, medicine and engineering (Haddad et al., 2010). An essential feature is that their state-variables, typically modelling abundances or concentrations, are necessarily nonnegative. The theory of *linear* positive dynamical systems is rooted in the seminal work of Perron and Frobenius in the early 1900s on nonnegative matrices (for a recent treatment see, for example, Berman and Plemmons (1994, Chapter 2)). Briefly, techniques such as comparison or monotonicity arguments are applicable when working with positive dynamical systems; arguments which need not hold in more general settings. Common linear Lyapunov functions for both discrete- and continuous-time positive systems have been considered in, for example, Hinrichsen and Plischke (2007), Knorn et al. (2009) and Fornasini and Valcher (2010; 2012) (and the references therein). Although there is some partial overlap between the techniques used in these papers and here, we have quite different emphases and potential applications.

A criticism of the model (1.1) is its linear structure or, biologically, its density-independence, which neglects any potential crowding, competition or Allee effects (Courchamp et al., 2008), and allows for unbounded exponential growth. Therefore, we also derive a necessary condition for DDG in the case where each patch has dynamics governed by a non-linear model. The models used here are known in systems & control theory as Lur’e (or Lurie) systems. Their name is attributed to the Soviet scientist and scholar Anatolii I. Lurie, one of the first, but by no means only, authors to study them, and who made significant early contributions to their development. In a biological context, these models allow both linear and non-linear vital rates, and exhibit a wider range of dynamic behaviour than linear models. Much attention has been devoted in the control theory literature to the study of Lur’e systems including, but not restricted to, Liberzon (2006), Jayawardhana et al. (2011) and Vidyasagar (2002). The dynamics of biologically motivated Lur’e systems have been addressed in, for example, Townley et al. (2012), Rebarber et al. (2011), Smith and Thieme (2013), Franco et al. (2014) and Eager et al. (2014b), see also particularly Eager (2016) for a helpful and informative discussion. As with the linear case, providing analytic conditions in terms of the model parameters for when DDG occurs in stage-structured non-linear models with a discrete patch structure is, at best, very specific to each example and, at worst, intractable. However, by appealing to absolute stability results from linear dissipativity theory (Haddad and Chellaboina, 2005; Haddad et al., 2003), we present a necessary condition for DDG again in terms of the non-existence of a candidate common linear Lyapunov function. Qualitatively the same results as those in the linear case apply.

The manuscript is organised as follows. After recording some notation, Sections 2 and 3 form the heart of the manuscript and consider DDG in population models with a discrete-spatial structure in the two cases that each patch is assumed to have linear and non-linear dynamics, respectively. Our main results in Section 2 are Theorem 2.6 and Corollary 2.7. Section 4 is technical and demonstrates that the continuous-time versions of the results in the previous two sections hold, illustrating that our findings are not an artefact of a discrete-time modelling framework. The interpretation of these results is the same as their discrete-time counterparts. We provide a summary of our work and biological interpretation in Section 5. Lengthier proofs appear in the Appendix.

Notation: Most notation we use is standard. The symbols $\mathbb{N}$ and $\mathbb{R}$ denote the sets of positive integers and real numbers, respectively, and $\mathbb{N}_0 = \{0\} \cup \mathbb{N}$. For $n, m \in \mathbb{N}$, we let $\underline{n} := \{1, 2, \dots, n\}$, $\mathbb{R}^n$ and $\mathbb{R}^{n\times m}$ denote usual n-dimensional Euclidean space and the set of $n \times m$ matrices with real entries, respectively. The superscript ^{T} denotes both matrix and vector transposition. For $M, N \in \mathbb{R}^{n\times m}$ with entries m_{ij} and n_{ij}, respectively, we write

$$\begin{aligned} &M \le N \quad \text{if } m_{ij} \le n_{ij} \text{ for all } i \in \underline{n},\ j \in \underline{m},\\ &M < N \quad \text{if } M \le N \text{ and } M \neq N,\\ &M \ll N \quad \text{if } m_{ij} < n_{ij} \text{ for all } i \in \underline{n},\ j \in \underline{m}, \end{aligned}$$

with the obvious corresponding definitions for $\ge$, $>$ and $\gg$, respectively. We let $\mathbb{R}^{n\times m}_+$ denote the set of nonnegative matrices, that is, $M \in \mathbb{R}^{n\times m}_+$ if $0 \le M$. We call M positive or strictly positive if $0 < M$ or $0 \ll M$, respectively, noting that there are different conventions present in the academic literature for the term *positive matrix*. The symbols I and $\mathbb{1}$ denote the identity matrix and the vector with each component equal to one, respectively — the dimension of which shall be consistent with the context.

Given a square matrix $M \in \mathbb{R}^{n\times n}$, we let $r(M)$ denote the spectral radius of M which, recall, is given by

$$r(M) := \max\{|\lambda| \,:\, \lambda \in \sigma(M)\},$$

where $\sigma(M)$ denotes the set of eigenvalues of M. For $v \in \mathbb{R}^n$, $\|v\|$, $\|M\|$ and $\mathrm{col}_i(M)$ denote a (any) norm of v, the corresponding induced operator norm of M and the i-th column of M, respectively. We shall occasionally require the induced matrix one-norm, denoted $\|\cdot\|_1$. We recall that if M is additionally nonnegative, then M is irreducible if, and only if, for each $i, j \in \underline{n}$ there exists $k \in \mathbb{N}$ such that the (i, j)-th entry of M^k is positive. Irreducible matrices presently play a role as the celebrated Perron–Frobenius Theorem ensures that if M is irreducible, then $r(M) \in \sigma(M)$ and further, $r(M)$ is a simple eigenvalue with corresponding left and right eigenvectors which may be chosen strictly positive (from numerous possible references see, for example, Berman and Plemmons (1994, Theorem 1.4, p. 27)).

2. Dispersal driven growth for linear models

We begin by describing the class of linear discrete-time, discrete-patch models we consider, before reviewing the concept of dispersal driven growth (DDG) and then presenting a necessary condition for DDG.

2.1. Problem formulation

We consider the following model to describe a population across $m \in \mathbb{N}$ patches:

$$x_i(t+1) = A_i x_i(t) - D_i x_i(t) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij} D_j x_j(t), \quad x_i(0) = x_i^0, \qquad t \in \mathbb{N}_0, \quad i \in \underline{m}. \tag{2.1}$$

Here $x_i(t)$ denotes the population in the i-th patch at time-step t, for $i \in \underline{m}$. The vector $x_i(t)$ is partitioned into $n \in \mathbb{N}$ stage-classes and x_i^0 is the initial distribution on the i-th patch, which is necessarily (componentwise) nonnegative. The matrices $A_i \in \mathbb{R}^{n\times n}_+$ model the vital rates of the population in the i-th patch and D_i is a dispersal matrix associated with that patch. The terms γ_{ij} in (2.1) are nonnegative scalars taking values between zero and one which account for the proportion of the population which survives dispersal from patch j to patch i.

For a meaningful mathematical model, we record the following assumptions for the terms which appear in (2.1):

(A1) $A_i, D_i, A_i - D_i \ge 0$, for every $i \in \underline{m}$;
(A2) $\gamma_{ij} \in [0, 1]$ and $\sum_{\substack{k=1\\ k\neq j}}^{m} \gamma_{kj} \in [0, 1]$, for every $i, j \in \underline{m}$.

The first assumption ensures that (2.1) always predicts nonnegative populations, and the second guarantees that dispersal is not a creative process. Moreover, the sum in (A2) may be less than one which then models a mortality rate associated with dispersal.

We are primarily interested in exploring the situation wherein each patch is a deterministic sink, yet cumulatively the dispersal model may demonstrate growth. To that end, we record the third assumption:

(A3) $r(A_i) < 1$, for every $i \in \underline{m}$.

The dispersal model (2.1) may equivalently be expressed in the block form

$$\begin{bmatrix} x_1(t+1)\\ x_2(t+1)\\ \vdots\\ x_m(t+1)\end{bmatrix} = \begin{bmatrix} A_1 - D_1 & \gamma_{12}D_2 & \dots & \gamma_{1m}D_m\\ \gamma_{21}D_1 & A_2 - D_2 & \ddots & \gamma_{2m}D_m\\ \vdots & & \ddots & \vdots\\ \gamma_{m1}D_1 & \dots & \ddots & A_m - D_m \end{bmatrix} \begin{bmatrix} x_1(t)\\ x_2(t)\\ \vdots\\ x_m(t)\end{bmatrix}, \quad \begin{bmatrix} x_1(0)\\ x_2(0)\\ \vdots\\ x_m(0)\end{bmatrix} = \begin{bmatrix} x_1^0\\ x_2^0\\ \vdots\\ x_m^0\end{bmatrix}, \quad t \in \mathbb{N}_0. \tag{2.2}$$

Evidently, zero is an equilibrium of (2.1), corresponding to population absence. Moreover, if no dispersal is present, meaning $D_i = 0$ for every $i \in \underline{m}$, then (2.1) or (2.2) reduces to m versions of (1.1), each with the matrix A in (1.1) replaced by A_i. Assumption (A3) then implies that $x_i(t) \to 0$ as $t \to \infty$ for every x_i^0 and every $i \in \underline{m}$ so that, in particular, the zero equilibrium of (2.1) is globally asymptotically stable. The next definition records what we mean by dispersal driven growth.

Definition 2.1. We say that the dispersal model (2.1) under assumptions (A1)–(A3) demonstrates dispersal driven growth if the zero equilibrium is not globally asymptotically stable.

2.2. When does dispersal driven growth occur?

Given the dispersal model (2.1), let $\mathcal{A}$ denote the block matrix in (2.2). In the present linear setting, DDG occurs precisely when $r(\mathcal{A}) \ge 1$. A consequence of assumption (A1) is that $\mathcal{A} \ge 0$ and so $r(\mathcal{A})$ is an eigenvalue of $\mathcal{A}$. Let $\mathcal{A}_0$ denote the block diagonal matrix:

$$\mathcal{A}_0 := \begin{bmatrix} A_1 & 0 & \dots & & 0\\ 0 & A_2 & 0 & \dots & \vdots\\ 0 & \dots & \ddots & \ddots & \vdots\\ 0 & \dots & \dots & \ddots & 0\\ 0 & \dots & \dots & 0 & A_m \end{bmatrix}$$

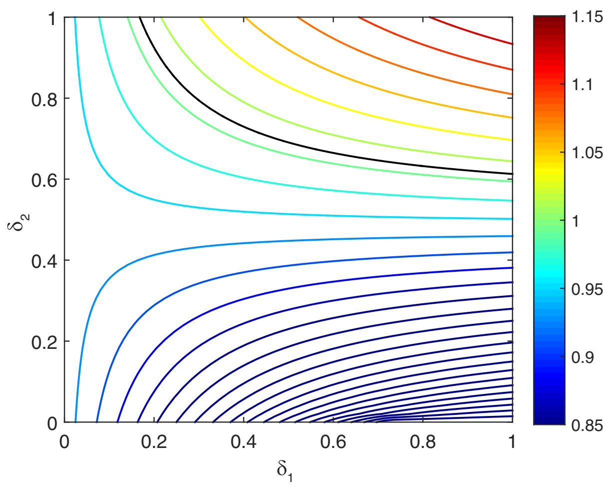

Fig. 2.1. Contour plot of $r(\mathcal{A})$ from (2.2) against parameters δ_1 and δ_2. Model data is as in (2.3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$\text{so that} \quad r(\mathcal{A}_0) = \max\left\{r(A_1), \ldots, r(A_m)\right\} < 1\,,$$

when (A3) holds. In the absence of dispersal, $\mathcal{A} = \mathcal{A}_0$ and so $r(\mathcal{A}) = r(\mathcal{A}_0) < 1$. The example below illustrates that the inclusion of non-zero dispersal terms in $\mathcal{A}$ may cause $r(\mathcal{A})$ to exceed the DDG threshold of $r(\mathcal{A}) = 1$, that is, the model (2.1) may exhibit dispersal driven growth.

Example 2.2. Take $m = 2$ and $n = 3$ and consider (2.1) with

$$\left.\begin{array}{l} A_1 = \begin{bmatrix} 0.06 & 1.16 & 3.29 \\ 0.65 & 0 & 0 \\ 0 & 0.03 & 0.05 \end{bmatrix}, \quad D_1 = \begin{bmatrix} 0 & 0 & 0 \\ 0.65 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \\ A_2 = \begin{bmatrix} 0.41 & 0.02 & 0.03 \\ 0.18 & 0.39 & 0 \\ 0 & 0.41 & 0.35 \end{bmatrix}, \quad D_2 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0.41 & 0 \end{bmatrix} \end{array}\right\} \tag{2.3}$$

and where $\gamma_{21} = \delta_1$ and $\gamma_{12} = \delta_2$ are parameters. The matrices A_1 and A_2 are taken from Davis and Levin (2002, pp.243–244) as matrix population projection models for US populations of woolly sculpin at different sites. The spectral radii are $r(A_1) = 0.9394$ and $r(A_2) = 0.5272$, evidently both less than one. The contour plot in Fig. 2.1 shows contours of constant spectral radius of $\mathcal{A}$ (the block matrix in (2.2)) as the parameters δ_1 and δ_2 vary. Here $\delta_i = 0$ denotes no dispersal and $\delta_i = 1$ denotes dispersal (and survival) of everything from that stage-class, for $i \in \{1, 2\}$. The black contour denotes the parameter values for which the spectral radius is equal to one. The region to the right and above the black contour give values of the parameters where dispersal driven growth takes place. We note the asymmetry between δ_1 and δ_2: δ_1 may be as low as 0.2 if δ_2 is sufficiently large, in part, we suspect paralleling the fact that $r(A_2)$ is much smaller than $r(A_1)$ in this example. ◊

In certain, rather particular, cases we are able to make assertions about $r(\mathcal{A})$ based on the structure of $\mathcal{A}$ alone.

Lemma 2.3. *Given the dispersal model (2.1) satisfying assumptions (A1)–(A3), DDG is not possible if dispersal is uni-directional in the sense that $\gamma_{ij} = 0$ for all $i < j$ (or $i > j$), for any dispersal matrices $\{D_1, \ldots, D_m\}$.*

Proof. Either set of assumptions leads to the block matrix in (2.2) being block triangular, so that the spectral radius is determined by the diagonal blocks. For example, if $\gamma_{ij} = 0$ for all $i > j$, then

$$\mathcal{A} = \begin{bmatrix} A_1 - D_1 & \gamma_{12} D_2 & \cdots & \gamma_{1m} D_m \\ 0 & A_2 - D_2 & \ddots & \gamma_{2m} D_m \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & A_m - D_m \end{bmatrix},$$

and thus

$$r(\mathcal{A}) = \max_{i \in \underline{m}} \left\{r(A_i - D_i)\right\} \le \max_{i \in \underline{m}} \left\{r(A_i)\right\} < 1\,,$$

where we have used the monotonicity of the spectral radius; see, for example, Berman and Plemmons (1994, p.27). It follows that the zero equilibrium of (2.1) is globally exponentially stable and DDG is not possible. The case when $\gamma_{ij} = 0$ for all $i < j$ is proven similarly. □

We emphasise the point that, of course, given $\{A_1, \ldots, A_m\}$, $\{D_1, \ldots, D_m\}$ and γ_{ij}, the leading eigenvalue $r(\mathcal{A})$ may be computed numerically. However, apart from a few special cases such as Lemma 2.3 above, computing eigenvalues alone does not yield much insight into the interplay between biological and dispersal processes, or the patch network structure and the onset of DDG, which is rather unsatisfactory. The field of describing the effects of perturbations on matrices is known broadly as perturbation theory. Matrices and eigenvalues are such ubiquitous objects, appearing throughout engineering, mathematics and science, that perturbation theory is a mature subject; see, for example, Stewart and Sun (1990) and Kato (1995) or Wilkinson (1988), with different academic communities having developed their own theory. Within theoretical ecology, we are aware of two frameworks which may be used to describe how $r(\mathcal{A})$ depends on the model data: $\{A_1, \ldots, A_m\}$, $\{D_1, \ldots, D_m\}$ and γ_{ij}. The first appeals to sensitivity (Demetrius, 1969) (or elasticity (de Kroon et al., 1986)) analysis — using calculus to determine local rates of change, say of $r(\mathcal{A})$, with respect to various quantities, such as matrix entries. We refer the reader particularly to Hunter and Caswell (2005), as well as Caswell (2007) for similar techniques. The second seeks an analytic relationship between perturbation and effect (say on the spectral radius) suggested in this context in Hodgson and Townley (2004) and Hodgson et al. (2006). The reader is referred to Lubben et al. (2009) as well. The latter approach is based on the so-called stability radius, introduced in a robust control theoretic setting by Hinrichsen and Pritchard (1986a; 1986b). We comment that the stability radius for positive systems (that is, where the matrices involved are componentwise nonnegative) has been well-studied by Hinrichsen and others in Lin and Antsaklis (2009), Hinrichsen and Son (1998) and Son and Hinrichsen (1996).

It is beyond the scope, and not the purpose, of the present manuscript to bring the wealth of perturbation theory available to describe how $\mathcal{A}$ and particularly $r(\mathcal{A})$, in fullest generality, depend on $\{\mathcal{A}_1, \ldots, \mathcal{A}_m\}$, $\{D_1, \ldots, D_m\}$ and γ_{ij} — there are too many degrees of freedom for a concise treatment. Instead, we motivate these tools' utility by applying them to an example.

Example 2.4. Consider (2.1) in the special case that $m = 2$, $D_1 = d_1 e_1^T$, $D_2 = d_2 e_2^T$, for vectors $d_i, e_i \in \mathbb{R}^n_+$, $i \in \{1, 2\}$ (meaning that the dispersal matrices D_i both have rank one). Assuming that A_i, d_i and e_i^T are known and the assumptions $A_i - d_i e_i^T \ge 0$ and $r(A_i) < 1$ hold for $i \in \{1, 2\}$, we seek to describe the relationship between the eigenvalues of

$$\mathcal{A} = \begin{bmatrix} A_1 - D_1 & \gamma_{12} D_2 \\ \gamma_{21} D_1 & A_2 - D_2 \end{bmatrix} = \begin{bmatrix} A_1 - d_1 e_1^T & \delta_2 d_2 e_2^T \\ \delta_1 d_1 e_1^T & A_2 - d_2 e_2^T \end{bmatrix}, \tag{2.4}$$

and the dispersal survival parameters $\delta_1 := \gamma_{21} \in [0, 1]$ and $\delta_2 := \gamma_{12} \in [0, 1]$ with the aim of determining if or when DDG occurs.

Writing

$$\mathsf{A} := \begin{bmatrix} A_1 - d_1 e_1^T & 0 \\ 0 & A_2 - d_2 e_2^T \end{bmatrix}, \quad \mathsf{D} := \begin{bmatrix} d_2 & 0 \\ 0 & d_1 \end{bmatrix},$$
$$\Delta := \begin{bmatrix} \delta_2 & 0 \\ 0 & \delta_1 \end{bmatrix}, \quad \mathsf{E} := \begin{bmatrix} 0 & e_2^T \\ e_1^T & 0 \end{bmatrix},$$

we have that $\mathcal{A} = \mathsf{A} + \mathsf{D}\Delta\mathsf{E}$ and $1 \in \sigma(\mathcal{A})$ if, and only if, there exists $v \in \mathbb{R}^{2n}$, $v \neq 0$ such that $\mathcal{A}v = v$. Noting that $1 \notin \sigma(\mathsf{A})$, we may rearrange $\mathcal{A}v = v$ to give

$$\mathsf{E}(I - \mathsf{A})^{-1}\mathsf{D}\Delta\mathsf{E}v = \mathsf{E}v,$$

and as $\mathsf{E}v \neq 0$ (else $\mathcal{A}v = \mathsf{A}v = v$, which is false as $v \neq 0$ and $1 \notin \sigma(\mathsf{A})$), it follows that $1 \in \sigma(\mathsf{E}(I - \mathsf{A})^{-1}\mathsf{D}\Delta)$. The converse is also true. Observe that the problem of determining an eigenvalue of the $2n \times 2n$ matrix $\mathcal{A}$ has been reduced to that of determining an eigenvalue of the 2×2 (the rank of the perturbation $\mathsf{D}\Delta\mathsf{E}$) matrix $\mathsf{E}(I - \mathsf{A})^{-1}\mathsf{D}\Delta$. Thus there exists $w_1, w_2 \in \mathbb{R}$ such that

$$\begin{aligned} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix} &= \mathsf{E}(I - \mathsf{A})^{-1}\mathsf{D}\begin{bmatrix} w_1 \\ w_2 \end{bmatrix} \\ &= \begin{bmatrix} 0 & e_2^T \\ e_1^T & 0 \end{bmatrix}\begin{bmatrix} (I - (A_1 - d_1 e_1^T))^{-1} & 0 \\ 0 & (I - (A_2 - d_2 e_2^T))^{-1} \end{bmatrix} \\ &\quad \times \begin{bmatrix} d_2 & 0 \\ 0 & d_1 \end{bmatrix}\begin{bmatrix} w_1 \\ w_2 \end{bmatrix}. \end{aligned} \tag{2.5}$$

Defining the scalar-valued functions by $g_1, g_2 : [1, \infty) \to \mathbb{R}_+$ by

$$g_1(\lambda) : = e_1^T(\lambda I - (A_1 - d_1 e_1^T))^{-1} d_2 \geq 0 \quad \text{and}$$
$$g_2(\lambda) : = e_2^T(\lambda I - (A_2 - d_2 e_2^T))^{-1} d_1 \geq 0,$$

a routine simplification of (2.5) shows that $1 \in \sigma(\mathcal{A})$ if, and only if,

$$\delta_1\delta_2 g_1(1) g_2(1) = 1. \tag{2.6}$$

Moreover, straightforward adjustments to the above arguments yield that $1 \leq \lambda \in \sigma(\mathcal{A})$ if, and only if

$$\delta_1\delta_2 g_1(\lambda) g_2(\lambda) = 1.$$

Given that $0 \leq \delta_1, \delta_2 \leq 1$, we see immediately that the product $\delta_1\delta_2$ must be sufficiently large for DDG to occur. Since $\delta_1, \delta_2 \in [0, 1]$, we also require that $1/(g_1(1)g_2(1)) \in (0, 1]$ for DDG to be possible. Indeed, the case that $\delta_1 = 0$ or $\delta_2 = 0$ corresponds to unilateral dispersal, where we already know by Lemma 2.3 that DDG is not possible. Furthermore, it is readily proven that the functions g_1, g_2 are non-increasing with $g_i(\lambda) \to 0$ as $\lambda \to \infty$. Thus, the dispersal survival parameters δ_1, δ_2 must correspondingly increase for a growth rate $\lambda \geq 1$ to be exhibited in (2.1).

As a numerical example, we reconsider (2.3) and note that

$$D_1 = d_1 e_1^T \quad \text{with} \quad d_1 = \begin{bmatrix} 0 \\ 0.65 \\ 0 \end{bmatrix}, \; e_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix},$$

$$D_2 = d_2 e_2^T \quad \text{with} \quad d_2 = \begin{bmatrix} 0 \\ 0 \\ 0.41 \end{bmatrix}, \; e_2 = \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix},$$

so that $\mathcal{A}$ from (2.2) is in the form (2.4). Appealing to (2.6), a computation shows that

$$g_1(1) = 1.5105 \quad \text{and}$$
$$g_2(1) = 1.0763 \quad \Rightarrow \quad 1/(g_1(1)g_2(1)) = 0.6151.$$

In particular, DDG occurs in the dispersal model (2.1) with data (2.3) when the product $\delta_1\delta_2$ is no less than 0.6151. The line $\delta_1\delta_2 = 0.6151$ is, in fact, the same as the black line in Fig. 2.1.◊

The methods used in Example 2.4 of course extend to more general forms of (2.1), although an analytic relationship as simple as (2.6) may not always be achievable. We refer the reader to Hodgson and Townley (2004), Hodgson et al. (2006) and Lubben et al. (2009) for more examples of this approach.

As we have hopefully suggested, tools from perturbation theory may simplify the dependence of $r(\mathcal{A})$ on $\{A_1, \ldots, A_m\}$, $\{D_1, \ldots, D_m\}$ and γ_{ij} but, in its fullest generality, this is still a large problem. These considerations have led to the main contribution of the present manuscript — a simple test for ruling out DDG, which we proceed to describe.

2.3. A necessary condition for dispersal driven growth

The material which follows is predicated on common linear Lyapunov functions, also known as a *(common) linear copositive Lyapunov functions* (Briat, 2013) and the references therein, or by the term *linearly stable* (Hinrichsen and Plischke, 2007).

Definition 2.5. A set of nonnegative matrices $\{A_1, \ldots, A_m\} \subseteq \mathbb{R}_+^{n\times n}$ admits a common linear Lyapunov function (CLLF) if there exists a strictly positive $v \in \mathbb{R}_+^n$ and $\varepsilon \in (0, 1)$ such that

$$v^T A_i \leq \varepsilon v^T, \quad \forall\, i \in \underline{m}. \tag{2.7}$$

By way of commentary, if $\{A_1, \ldots, A_m\}$ admit a CLLF, then it follows from, for example, Krasnosel'skij et al. (1989, Lemma 16.1) that (A3) certainly holds. The converse is not true, and hence the terminology *common* — the property (2.7) is enjoyed by each of the A_i for the same v. Note also that the above definition is equivalent to: there exists a strictly positive $v \in \mathbb{R}_+^n$ such that

$$v^T A_i \ll v^T, \quad \forall\, i \in \underline{m}.$$

The next result is the main result of this section and states that existence of a CLLF for $\{A_1, \ldots, A_m\}$ means that DDG in (2.1) is not possible, irrespective of the dispersal terms.

Theorem 2.6. *If $\{A_1, \ldots, A_m\}$ admits a common linear Lyapunov function, then the zero equilibrium of the dispersal model (2.1) is globally exponentially stable, for all dispersal matrices $\{D_1, \ldots, D_m\}$ and for all weightings (γ_{ij}) which satisfy assumptions (A1)–(A2). Consequently, that $\{A_1, \ldots, A_m\}$ does not admit a CLLF is a necessary condition for DDG to occur.*

Proof. Let v^T denote a common linear Lyapunov function for $\{A_1, \ldots, A_m\}$ with $\varepsilon \in (0, 1)$ as in (2.7). Define

$$W : \mathbb{R}_+^{nm} \to \mathbb{R}_+, \quad W((z_1, \ldots, z_m)) := \sum_{i=1}^m v^T z_i, \tag{2.8}$$

and let $x := (x_1, \ldots, x_m)$ denote the solution of (2.1). We note that our assumptions (A1) and (A2) ensure that $x_i(t) \geq 0$ for each $t \in \mathbb{N}_0$ and thus $x(t) \in \mathbb{R}_+^{nm}$ for each $t \in \mathbb{N}_0$. For $t \in \mathbb{N}_0$, we estimate that

$$\begin{aligned} W(x(t+1)) &= \sum_{i=1}^m v^T x_i(t+1) \\ &= \sum_{i=1}^m v^T \Big[A_i x_i(t) - D_i x_i(t) + \sum_{\substack{j=1 \\ j\neq i}}^m \gamma_{ij} D_j x_j(t) \Big] \\ &= \sum_{i=1}^m v^T A_i x_i(t) - \sum_{i=1}^m v^T D_i x_i(t) + \sum_{j=1}^m \Big(\sum_{\substack{i=1 \\ i\neq j}}^m \gamma_{ij} \Big) v^T D_j x_j(t) \end{aligned}$$

$$
\begin{aligned}
&\leq \sum_{i=1}^{m} v^T A_i x_i(t) - \sum_{i=1}^{m} v^T D_i x_i(t) \\
&\quad + \sum_{j=1}^{m} v^T D_j x_j(t), \quad \text{by assumption A2} \\
&= \sum_{i=1}^{m} v^T A_i x_i(t) \leq \varepsilon \sum_{i=1}^{m} v^T x_i(t), \quad \text{by (2.7)} \\
&= \varepsilon W(x(t)).
\end{aligned} \tag{2.9}
$$

We conclude from the difference inequality (2.9) that for $t \in \mathbb{N}_0$

$$0 \leq W(x(t)) \leq \varepsilon^t W(x(0)) \to 0 \quad \text{as } t \to \infty. \tag{2.10}$$

Finally, since $0 \ll v$, we may estimate $W(z)$ by

$$\theta_1 \|z\| \leq W(z) \leq \theta_2 \|z\| \quad \forall\, z \in \mathbb{R}_+^{nm},$$

for some $0 < \theta_1 \leq \theta_2$ and so we conclude from (2.10) that $x(t) \to 0$ as $t \to \infty$, completing the proof. □

There are several immediate consequences of Theorem 2.6 which describe when DDG is not possible, which we formulate in the corollary below. Arguably, these observations would have been harder to establish without Theorem 2.6.

Corollary 2.7. *Given the dispersal model (2.1), assume that (A1)–(A3) hold.*

(1) *DDG is not possible in scalar models, that is, where the $A_i \in [0, 1)$ are scalar, $i \in \underline{m}$.*
(2) *DDG is not possible in models where the set of matrices $\{A_1, \ldots, A_m\}$ commute, and at least one of the A_i is irreducible.*
(3) *DDG is not possible in models where the patch dynamics are identical and irreducible, meaning that $\{A_1, \ldots, A_m\} = \{A\}$ for an irreducible A.*
(4) *For DDG to be possible, at least one of the A_i matrices must be "reactive", meaning that $\|A_j\|_1 \geq 1$ for some $j \in \underline{m}$.*
(5) *DDG is not possible if the set of matrices $\{A_1, \ldots, A_m\}$ has a maximal element which is irreducible, meaning that there exists $k \in \underline{m}$ such that $A_i \leq A_k$ for all $i \in \underline{m}$, and A_k is irreducible.*
(6) *Knowledge that $\{A_1, \ldots, A_m\}$ does not admit a CLLF is not, by itself, enough information to determine whether DDG occurs in (2.1).*

The irreducibility assumption in statements (3) and (5) has been imposed as a technical assumption to aid the proofs of these claims. It is not necessary in either case, and may be relaxed to: there exists a strictly positive $v \in \mathbb{R}_+^n$ and $\varepsilon \in (0, 1)$ such that $v^T A \leq \varepsilon v^T$ or $v^T A_k \leq \varepsilon v^T$ in statements (3) or (5), respectively. We note, however, that irreducibility is a realistic assumption for numerous empirically derived matrix population projection models available in the literature, see Stott et al. (2010), and so does not seem overly restrictive.

Proof of Corollary 2.7. (1): A set of scalars $\{A_1, \ldots, A_m\}$ with the property that $r(A_j) = A_j < 1$ for each $j \in \underline{m}$ (by assumption (A3)) certainly admits the common linear Lyapunov function $v = 1$. We note that the same conclusion could have also been derived in this special case by observing that the column sums of the nonnegative matrix in (2.2) are all less than one.

(2): It follows from, for example Krasnosel'skij et al. (1989, Lemma 9.6, p. 99), that if the family $\{A_1, \ldots, A_m\}$ commutes, then the A_i admit a common left nonnegative eigenvector, denoted v^T. Since at least one of the A_i is assumed irreducible, it follows from the Perron-Frobenius Theorem that in fact $v^T \gg 0$. Finally, assumption (A3) implies that v^T is a CLLF for $\{A_1, \ldots, A_m\}$.

(3): The claim follows immediately from (2), as every matrix trivially commutes with itself.

(4): Recall that the induced one-norm $\|M\|_1$ of a nonnegative matrix M is equal to the largest column sum of M. The vector of column sums of M is given by $\mathbb{1}^T M$. Thus if $\|A_i\|_1 < 1$ for all $i \in \underline{m}$, then $\mathbb{1}^T \gg 0$ is a CLLF for $\{A_1, \ldots, A_m\}$.

(5): Let v^T denote the simple, positive (up to scalar multiplication) left eigenvector of A_k corresponding to the eigenvalue $r(A_k)$, the existence of which is ensured by the Perron-Frobenius Theorem. Note that $r(A_k) < 1$, by (A3). Then for each $i \in \underline{m}$, $v^T A_i \leq v^T A_k \leq r(A_k) v^T$ and hence v^T is a CLLF for $\{A_1, \ldots, A_m\}$.

(6): It suffices to find an example. The set $\{A_1, A_2\}$ in (2.3) does not admit a CLLF. For the dispersal matrices $\{D_1, D_2\}$ also in (2.3), the condition (2.6) demonstrates that DDG occurs for $\delta_1 \delta_2$ sufficiently large, and not if $\delta_1 \delta_2$ is sufficiently small. □

We conclude this subsection with some examples.

Example 2.8. A matrix projection model for the peregrine falcon (*Falco peregrinus anatum*) was derived in Wootton and Bell (1992) (and also studied in Hunter and Caswell (2005)). The model describes a population with patch dynamics over two locations (representing northern and southern California). On each patch the population is modelled with two stage-classes (denoting juveniles and adults, respectively), with projection matrices:

$$A_1 = \begin{bmatrix} 0 & 0.2556 \\ 0.72 & 0.77 \end{bmatrix} \quad \text{and} \quad A_2 = \begin{bmatrix} 0 & 0.1908 \\ 0.72 & 0.77 \end{bmatrix}.$$

Each patch is asymptotically declining, as $r(A_1) = 0.9614 < 1$ and $r(A_2) = 0.9194 < 1$. Noting that $A_2 \leq A_1$, it follows from statement (5) of Corollary 2.7 that DDG is not possible in this model. From a conservation perspective, the model suggests that dispersal alone cannot asymptotically bring the population to stasis or growth and either a reintroduction scheme is required, or efforts should be concentrated on improving the quality of the patches (leading to an increase in $r(A_i)$).◊

Example 2.9. The result (Fornasini and Valcher, 2012, Theorem 1) contains necessary and sufficient conditions for when a set of nonnegative matrices $\{A_1, \ldots, A_m\}$ admits a CLLF which may be checked in examples. Specifically, from Fornasini and Valcher (2012, Theorem 1), it follows that $\{A_1, \ldots, A_m\}$ admits a CLLF if, and only if, for all $\pi\colon \underline{n} \to \underline{m}$

$$\mathcal{A}_\pi := [\mathrm{col}_1(A_{\pi(1)}), \mathrm{col}_2(A_{\pi(2)}), \ldots, \mathrm{col}_n(A_{\pi(n)})] \in \mathbb{R}_+^{n \times n},$$

satisfies $r(\mathcal{A}_\pi) < 1$. In words, every matrix formed from ordered columns of every possible combination of the matrices of A_j must have spectral radius less than one. There are m^n such matrices. Although exhaustive, the above test is computationally expensive when m and n are large, and a quicker (although not exhaustive) method is to search for a CLLF by solving the linear program: fix $\varepsilon \in (0, 1)$ and $0 < \kappa_1 < \kappa_2$ and seek to solve

$$\min_{v \in \mathbb{R}^n} \mathbb{1}^T v \quad \text{subject to} \quad \begin{bmatrix} A_1^T - \varepsilon I \\ \vdots \\ A_m^T - \varepsilon I \end{bmatrix} v \leq 0 \quad \text{and} \quad \kappa_1 \mathbb{1} \leq v \leq \kappa_2 \mathbb{1}.$$

Note that as CLLFs are invariant under multiplication by positive scalars, the choice of positive κ_1 and κ_2 is arbitrary. The inclusion of the bound $v \leq \kappa_2 \mathbb{1}$ is a conditioning property to ensure that v remains "reasonably" bounded. Further, if (v^T, ε_0) satisfy (2.7), then certainly (v^T, ε) do as well for all $\varepsilon \in (\varepsilon_0, 1)$. Therefore, since the size of ε makes no qualitative difference in Theorem 2.6 and its extensions, it is reasonable in practice to choose ε "very close to one". ◊

Example 2.10. The viability of the endangered plant species blowout penstemon (*Penstemon haydenii*), a perennial plant species which is endemic to the Sandhills of Nebraska and the northeast Great Divide Basin in Wyoming, is considered in the Ph.D. thesis of Kottas (2012) (see also Eager et al., 2014a). The habitat of Blowout penstemon is limited to so-called blowouts — depressions or eroded areas on hillsides. As a dispersal specialist, newly formed blowouts may be colonised by penstemon from existing populations. Quoting (Eager et al., 2014a): "The viability of penstemon is dependent on blowout suitability, particularly the formation of vegetative cover, as above–ground penstemon cannot persist in an environment consisting largely of grasses which have compact growth and an efficient root system". Changing agricultural practices which historically and periodically reduced vegetative cover and created new blowouts have put pressure on current penstemon populations. Yet another pressure on penstemon dispersal is a reduction of the frequency of fires which themselves aid dispersal by clearing other vegetation and creating bare sand which is easily blown by wind.

The viability of penstemon populations across a spatial region may be explored theoretically by adopting a discrete patch model, with patches denoting distinct blowouts, and stage-structured matrix models, with matrices A_i, modelling the population within in each blowout. That is, the model (2.1) may be used, where the terms D_i model dispersal between blowouts. Suitability of blowouts may be captured by A_i, particularly $r(A_i)$, and $r(A_i) < 1$ and $r(A_i) > 1$ corresponds to blowouts which are (asymptotic) sinks or sources, respectively.

Matrix models for penstemon are presented in Kottas (2012, Table 5.7, p. 232), each with four stage-classes denoting the seedbank, juvenile, adult and vegetative adult, respectively. Matrices are parameterised for 11 different blowouts and four of these matrices have spectral radius greater than one. The present example seeks to illustrate our results and, in the current context, investigate whether persistence of penstemon populations is possible via DDG. To that end, the matrices for blowouts CL168 and E1, with spectral radii 0.84 and 0.8, respectively, are given by

$$\begin{bmatrix} 0.003 & 0 & 0.624 & 0 \\ 0.008 & 0.353 & 2 & 0 \\ 0 & 0.127 & 0.3 & 0.25 \\ 0 & 0 & 0.025 & 0.25 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0.003 & 0 & 0.624 & 0 \\ 0.008 & 0.454 & 1.243 & 0 \\ 0 & 0.09 & 0.338 & 0.17 \\ 0 & 0 & 0.324 & 0.407 \end{bmatrix}.$$

With A_1 and A_2 denoting the respective matrices above, the Matlab (MATLAB and Statistics Toolbox Release, 2014a) code

```
n = 4; kappa1 = 0.1; kappa2 = 1; ep = 0.98;
f = ones(1,n); A = [A1'-ep*eye(n); A2'-ep*eye(n)];
v = linprog(f, A,zeros(2*n,1),[],[],
    kappa1*ones(n,1), kappa2*ones(n,1));
```

gives $v^T = [0.1\ 0.1\ 0.3908\ 0.1338]$, which (by construction) is a CLLF for $\{A_1, A_2\}$. Consequently, DDG is not possible between blowouts CL168 and E1. However, the matrices for blowouts E3 and G3, given by

$$\begin{bmatrix} 0.003 & 0 & 0.624 & 0 \\ 0.008 & 0.251 & 1.385 & 0 \\ 0 & 0.229 & 0.427 & 0.15 \\ 0 & 0 & 0.156 & 0.1 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0.003 & 0 & 0.258 & 0 \\ 0.008 & 0.633 & 0.903 & 0 \\ 0 & 0.079 & 0.736 & 0 \\ 0 & 0 & 0.264 & 0.75 \end{bmatrix},$$

with spectral radii 0.9266 and 0.9568, respectively, do not admit a CLLF as

$$[\mathrm{col}_1(A_1), \mathrm{col}_2(A_1), \mathrm{col}_3(A_2), \mathrm{col}_4(A_1)] = \begin{bmatrix} 0.003 & 0 & 0.258 & 0 \\ 0.008 & 0.251 & 0.903 & 0 \\ 0 & 0.229 & 0.736 & 0.15 \\ 0 & 0 & 0.264 & 0.1 \end{bmatrix},$$

has spectral radius $1.04 > 1$. Hence a CLLF does not exist (by Fornasini and Valcher (2012, Theorem 1)) and, therefore, we cannot rule out the possibility of DDG between blowouts E3 and G3. In fact, DDG is possible between these blowouts, theoretically suggesting that penstemon may persist via dispersal alone. For example, with D_1 and D_2 both equal to the four by four zero matrix apart from entries (3, 2) and (2, 3) with values 0.2107 and 0.8308, respectively, it follows that (A1)–(A3) hold with $\gamma_{12} = \gamma_{21} = 1$ and $\mathcal{A}$ given by the block matrix in (2.2) has $r(\mathcal{A}) = 1.0008 > 1$. We comment that D_1 having a non-zero (3, 2) component means that at each time-step juvenile plants from $E3$ disperse (and grow) to the adult plant stage-class in $G3$, which may not occur by wind alone, but require other transport mechanisms. ◊

2.4. Further extensions to the necessary condition for dispersal driven growth

To summarise thus far, the asymptotics of the model (2.1) depend on the terms A_i (modelling biological processes), as well as the D_i and γ_{ij} (modelling dispersal processes). Theorem 2.6 demonstrates that the existence of a CLLF for $\{A_1, \dots, A_m\}$ prevents DDG from occurring, *independently* of the dispersal terms D_i and γ_{ij}. The proof of Theorem 2.6 in fact indicates that a stronger result is true: if $\{A_1, \dots, A_m\}$ admits a CLLF, then DDG is not possible even when a more complicated mathematical form is adopted for modelling dispersal, such as assuming that dispersal is time-varying, delayed or non-linear — the first claim we formulate as a corollary.

Corollary 2.11. *If $\{A_1, \dots, A_m\}$ admits a CLLF, then the zero equilibrium of the dispersal model*

$$x_i(t+1) = A_i x_i(t) - D_i(t)x_i(t) + \sum_{j \neq i} \gamma_{ij}(t) D_j(t) x_j(t),$$
$$x_i(0) = x_i^0, \quad t \in \mathbb{N}_0, \quad i \in \underline{m},$$

is globally exponentially stable, for all possibly time-varying dispersal matrix functions $\{D_1, \dots, D_m\}$ and for all weightings (γ_{ij}) which satisfy the assumptions:

(A1)′ A_i, $D_i(t)$, $A_i - D_i(t) \geq 0$, for every $i \in \underline{m}$ and $t \in \mathbb{N}_0$;
(A2)′ $\gamma_{ij}(t) \in [0, 1]$ and $\sum_{k=1, k \neq j}^{m} \gamma_{kj}(t) \in [0, 1]$, for every $i, j \in \underline{m}$ and $t \in \mathbb{N}_0$.

The proof of Corollary 2.11 is the same as that of Theorem 2.6, and is thus omitted.

Provided that the corresponding versions of assumptions (A1) and (A2) hold, the conclusions of Corollary 2.11 apply if dispersal in (2.1) is assumed to be subject to delays, that is $D_i x_i(t)$ is replaced by $D_i(t)x_i(t-\tau)$ for all $i \in \underline{m}, t \in \mathbb{N}_0$ and some $\tau \in \mathbb{N}_0$. For the sake of brevity we do not give a formal statement.

We have so far assumed that the patch dynamics are time-invariant (also known as autonomous). Time-varying matrix projection models allow for temporal variation in vital rates owing to demographic stochasticity or fluctuations. Our next result shows that if the set of nonnegative-valued matrix functions $\{A_1, \dots, A_m\}$ admits a CLLF *uniformly in time*, then again DDG is not possible in the now time-varying dispersal model (2.12). The proof is the same as that of Theorem 2.6.

Corollary 2.12. *If the set of matrix-valued functions $\{A_1, \dots, A_m\}$ admits a CLLF uniformly in time, meaning that there exists a strictly positive $v \in \mathbb{R}^n_+$ and $\varepsilon \in (0, 1)$ such that*

$$v^T A_i(t) \le \varepsilon v^T \quad i \in \underline{m},\ t \in \mathbb{N}_0\,, \tag{2.11}$$

then the zero equilibrium of the time-varying dispersal model

$$x_i(t+1) = A_i(t)x_i(t) - D_i(t)x_i(t) + \sum_{j \ne i} \gamma_{ij}(t) D_j(t) x_j(t),$$
$$x_i(0) = x_i^0, \quad t \in \mathbb{N}_0, \quad i \in \underline{m}, \tag{2.12}$$

is globally exponentially stable, for all dispersal matrix functions $\{D_1, \dots, D_m\}$ and for all weightings (γ_{ij}) which satisfy the assumptions:

(A1)″ $A_i(t)$, $D_i(t)$, $A_i(t) - D_i(t) \ge 0$, for every $i \in \underline{m}$ and $t \in \mathbb{N}_0$;

and (A2)′.

Remark 2.13.

(a) The conclusions of Corollary 2.12 still hold if the condition (2.11) is relaxed to
$$\limsup_{t\to\infty} v^T A_i(t) \le \varepsilon v^T \quad i \in \underline{m}\,,$$
roughly meaning that the CLLF for $\{A_1, \dots, A_m\}$ need only exist uniformly for large enough times.

(b) A downside with using Corollary 2.12 practically is that establishing whether condition (2.11) holds requires verifying infinitely many inequalities — a task compounded by the fact that in reality the A_i may not be known exactly. We mention two instances where it may be more readily checked. First, if the A_i are assumed periodic, then establishing (2.11) reduces to finding a (usual) CLLF for the larger, but finite, set $\{A_j(\tau)\}$ so that Fornasini and Valcher (2012, Theorem 1) applies, or a linear program may be used. Second, if $A_i(t) = B_i + \Delta_i(t)$ where the B_i admit a CLLF and the Δ_i are sufficiently "small", then (2.11) holds. □

The dispersal model (2.1) assumes that dispersal acts additively via addition and subtraction of the D_i terms. In certain situations, it may be more appropriate to model dispersal multiplicatively. To that end, for $m \in \mathbb{N}$ consider:

$$x_i(t+1) = A_i\Big[\Theta_i(t)x_i(t) + \sum_{j \ne i} \gamma_{ij}(t)(I - \Theta_j(t))x_j(t)\Big]$$
$$x_i(0) = x_i^0, \quad t \in \mathbb{N}_0, \quad i \in \underline{m}. \tag{2.13}$$

We assume that:

(B3)1 $A_i, \Theta_i(t) \in \mathbb{R}^{n\times n}_+$ and $\Theta_i(t)$ is diagonal with diagonal entries taking values in [0, 1] for every $i \in \underline{m}$ and $t \in \mathbb{N}_0$;

which ensures that $x_i(t) \ge 0$ for each $i \in \underline{m}$ and $t \in \mathbb{N}_0$. The term $\Theta_i(t)x_i(t)$ denotes the (possibly time-varying) proportion of the population of the i-th patch that remains in the i-th patch at time-step t. The remaining quantity $(I - \Theta_i(t))x_i(t)$ is assumed to disperse to other patches. The γ_{ij} appearing in (2.13) play the same role as in (2.1). The interpretation in (2.13) is that dispersal takes place across all patches before the biological processes, hence the products $A_i\Theta_i$ appear, instead of $\Theta_i A_i$.

The conclusion of the next corollary is the same as that of Theorem 2.6, namely; existence of a CLLF for $\{A_1, \dots, A_m\}$ prevents DDG from occurring in the multiplicative (or proportional) dispersal model (2.13).

Corollary 2.14. *If $\{A_1, \dots, A_m\}$ admits a common linear Lyapunov function, then the zero equilibrium of the dispersal model (2.13) is globally exponentially stable, for all dispersal matrix functions $\{\Theta_1, \dots, \Theta_m\}$ and for all weightings (γ_{ij}) which satisfy assumptions (A1)* and (A2)′.*

The proof of Corollary 2.14 is along the lines of that of Theorem 2.6, and hence is omitted.

We conclude the section by providing some commentary on another notion of common stability, and its relation to our necessary condition for DDG, and also how dispersal may be stabilising (the opposite phenomenon to DDG).

Remark 2.15. In deriving tests for DDG, we have explored the utility and application of common *linear* Lyapunov functions. Another mechanism for ensuring certain notions of common stability are so-called common *quadratic* Lyapunov functions — used in classical stability analysis of switched control systems; see, for instance, Liberzon and Morse (1999). We recall that the symmetric, positive definite $P \in \mathbb{R}^{n\times n}$ is a common quadratic Lyapunov function for the set $\{M_1, \dots, M_m\}$ of $n \times n$ (not necessarily nonnegative) matrices if there exists $\beta > 0$ such that

$$M_i^* P M_i - P \preccurlyeq -\beta I \quad i \in \underline{m}\,, \tag{2.14}$$

where the notation $X \preccurlyeq Y$ means that $Y - X$ is positive semi-definite and M^* denotes the conjugate transpose of M. The terminology quadratic Lyapunov function is used here as associated with P satisfying (2.14) is the quadratic functional $V : \mathbb{C}^n \to \mathbb{R}_+$, $V(w) = \langle w, Pw\rangle = w^T \overline{Pw}$ and (2.14) demonstrates that solutions z of

$$z(t+1) = M_{i(t)} z(t) \quad z(0) = z^0 \quad t \in \mathbb{N}_0\,,$$

converge to zero, for any "switching sequence" $i : \mathbb{N}_0 \to \underline{m}$.

A natural question to ask, therefore, is given the dispersal model (2.1) satisfying (A1)–(A3), does existence of a common quadratic Lyapunov function for $\{A_1, \dots, A_m\}$ rule out DDG? The answer is, in fact, no. The matrices

$$A_1 = \begin{bmatrix} 0.8 & 0.1 \\ 0.18 & 0.9 \end{bmatrix} \quad \text{and} \quad A_2 = \begin{bmatrix} 0.8 & 0.05 \\ 0.5 & 0.8 \end{bmatrix},$$

admit the common quadratic Lyapunov function

$$P = \begin{bmatrix} 488 & -55 \\ -55 & 166 \end{bmatrix},$$

yet the dispersal model (2.1) exhibits DDG with, for example,

$$D_1 = \begin{bmatrix} 0.36 & 0.0075 \\ 0.081 & 0.0675 \end{bmatrix}, \quad D_2 = \begin{bmatrix} 0.06 & 0.0225 \\ 0.0375 & 0.36 \end{bmatrix} \quad \text{and}$$
$$\gamma_{12} = \gamma_{21} = 1\,.$$

It is for this reason that we have focussed our attention on CLLFs for the set $\{A_1, \dots, A_m\}$ when designing a necessary condition for DDG. □

Remark 2.16. Throughout the present contribution we have focussed on how dispersal in matrix models with discrete patch dynamics may act to "destabilise" them — in the sense that the inclusion of dispersal terms causes the zero equilibrium to become unstable. Our motivating application is the potential consequences to population persistence via dispersal alone. For the sake of clarity, we comment that dispersal between two (or more) unstable matrices may be stabilising — the *opposite* effect of what we have termed DDG. As an example, the matrices

$$A_1 := \begin{bmatrix} 0.9 & 0.35 \\ 0.3 & 0.7 \end{bmatrix} \quad \text{and} \quad A_2 := \begin{bmatrix} 0.3 & 1.2 \\ 0.4 & 0.5 \end{bmatrix},$$

have $r(A_1) = 1.1391 > 1$ and $r(A_2) = 1.1 > 1$. However, the dispersal terms

$$D_1 := \begin{bmatrix} 0.5888 & 0.2163 \\ 0.0438 & 0.0310 \end{bmatrix} \quad \text{and} \quad D_2 := \begin{bmatrix} 0.1535 & 0.2657 \\ 0.3826 & 0.3967 \end{bmatrix},$$

satisfy (A1) yet cause

$$r\left(\begin{bmatrix} A_1 - D_1 & D_2 \\ D_1 & A_2 - D_2 \end{bmatrix}\right) = 0.9971 < 1\,.$$

This observation parallels the comments made in the Introduction, where we recalled that diffusion is widely recognised as "usually" being a stabilising process but can, for instance in reaction-diffusion equations, lead to instability.

Further, we note that dispersal in matrix models with discrete patch dynamics may act to "improve decline" without actually causing asymptotic stasis or growth. By that we mean, given $\{A_1, \dots, A_m\}$, $\{D_1, \dots, D_m\}$ and $(\gamma_{ij})_{ij}$ satisfying (A1)–(A3), let $\mathcal{A}$ denote the block matrix in (2.2). It is possible that

$$\max\left\{r(A_1), \dots, r(A_m)\right\} < r(\mathcal{A}) < 1\,, \tag{2.15}$$

so that the inclusion of dispersal has *raised* the asymptotic rate of decline of the matrix model, compared to that without dispersal, but that asymptotic stasis or growth still does not occur. We acknowledge that there are reasonable arguments as to why the phenomenon (2.15) may also be termed dispersal driven growth. We have chosen the current definition of DDG to capture the qualitatively different situation wherein stasis ($r(\mathcal{A}) = 1$) or growth ($r(\mathcal{A}) > 1$) arises as a consequence of dispersal. □

3. Dispersal driven growth for a class of non-linear models

We next consider models for populations with a discrete-spatial structure but where, in contrast to Section 2, the dynamics on each patch are assumed non-linear. As stated in the Introduction, the motivation for doing so is that the non-linear models we consider exhibit more varied and biologically realistic dynamic behaviour than the linear models used in Section 2.

The present section is organised as follows. We first introduce and motivate the models we shall use for the patch dynamics, and demonstrate numerically that DDG is possible when these models are coupled via dispersal, even when the zero equilibrium of each model is GES in isolation. Determining analytically when DDG occurs in the non-linear case is, in general, even less tractable than the linear case and so, in the spirit of Section 2, we provide a necessary condition for DDG to occur, which is readily checkable numerically. Our main result of this section is Theorem 3.2.

3.1. A class of non-linear models

Consider first the following single patch model

$$x(t+1) = Ax(t) + BF(Cx(t)), \quad x(0) = x^0,\ t \in \mathbb{N}_0\,. \tag{3.1}$$

As in Section 2, the vector $x(t) \in \mathbb{R}^n_+$ denotes the stratified population at time-step t, with n distinct stage-classes. The nonnegative $n \times n$ matrix A in (3.1) contains vital rates which are assumed density-independent, typically movement between stage-classes (such as growth or survival) and the second term on the right hand side of (3.1) models vital rates which are assumed density-dependent, typically recruitment. In this case, the $p \times n$ and $n \times \ell$ nonnegative matrices C and B capture the fecundities of the various stage-classes, and the distribution of new members into the population, respectively, for $p, \ell, n \in \mathbb{N}$. The function $F : \mathbb{R}^p_+ \to \mathbb{R}^\ell_+$ in (3.1) captures density-dependence and the components of F are typically sub-linear, such as a Holling type II (Holling, 1959) function (also known as a

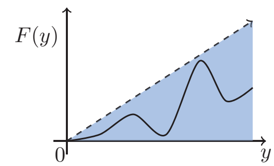

Fig. 3.1. Illustration of the sector condition (3.4) — the graph of F must lie within the shaded region, with boundary the straight line through (0,0) with slope q/r. A sample graph of such an F is plotted.

Beverton and Holt, 1957) or a (Ricker, 1954) non-linearity. We refer the reader to, for example, Townley et al. (2012), Rebarber et al. (2011) and Eager et al. (2014b) or Eager (2016) for more biological interpretation of models of the form (3.1).

When F in (3.1) satisfies $F(0) = 0$, then zero is an equilibrium of (3.1). If A, B, C are such that there exists nonnegative vectors $q \in \mathbb{R}^p_+$, $r \in \mathbb{R}^\ell_+$ and strictly positive $\rho \in \mathbb{R}^n_+$ such that

$$\rho^T A - \rho^T + q^T C \ll 0 \quad \text{and} \quad \rho^T B - r^T \ll 0\,, \tag{3.2}$$

then the zero equilibrium of the dispersal model (3.5) is globally exponentially stable (GES), for all functions $F : \mathbb{R}^p_+ \to \mathbb{R}^\ell_+$ which satisfy

$$r^T F(y) \le q^T y \quad \forall\, y \in \mathbb{R}^p_+\,. \tag{3.3}$$

By Krasnosel'skij et al. (1989, Lemma 16.1), the first inequality in (3.2) implies that $r(A) < 1$. When A only models movement within and between stage-classes (that is, not recruitment), $r(A) < 1$ is a reasonable requirement. The condition (3.3) is a linear constraint, as the weighted nonnegative linear combination of the components of $F(y)$, $r^T F(y)$, must be bounded by the weighted nonnegative linear combination of the components of y, $q^T y$. The terms r and q are related to the linear data A, B and C by the condition

$$r^T - q^T C(I - A)^{-1} B \gg 0\,,$$

which follows from (3.2). Note that $r(A) < 1$ implies that $I - A$ is invertible.

The simplest case to consider is when $p = \ell = 1$, so that r and q are scalars and F is scalar-valued. Then, assuming that $r > 0$, the condition (3.3) reduces to

$$0 \le F(y) \le \frac{q}{r} y \quad \forall\, y \in \mathbb{R}_+\,, \tag{3.4}$$

which constrains the graph of F to belong to the sector with slope q/r, as depicted in Fig. 3.1.

To augment (3.1) with a discrete-spatial structure and dispersal, we consider the following model:

$$x_i(t+1) = A_i x_i(t) + B_i F_i(C_i x_i(t)) - D_i(x_i(t)) + \sum_{\substack{j=1 \\ j \ne i}}^{m} \gamma_{ij}(t) D_j(x_j(t)),\ x_i(0) = x_i^0,\ t \in \mathbb{N}_0,\ i \in \underline{m}, \tag{3.5}$$

where $m \in \mathbb{N}$ and we assume that:

(B1) $A_i \in \mathbb{R}^{n \times n}_+$, $B_i \in \mathbb{R}^{n \times \ell}_+$, $C_i \in \mathbb{R}^{p \times n}_+$ for $n, \ell, p \in \mathbb{N}$ and all $i \in \underline{m}$;
(B2) $F_i : \mathbb{R}^p_+ \to \mathbb{R}^\ell_+$ for $i \in \underline{m}$.

The terms D_i again model dispersal and are now assumed functions $D_i : \mathbb{R}^n_+ \to \mathbb{R}^n_+$. For a meaningful mathematical model of nonnegative populations we further assume that:

(B3) $A_i x + B_i F_i(C_i x) - D_i(x) \ge 0$, for all $x \in \mathbb{R}^n_+$ and $i \in \underline{m}$,

implying that $x_i(t) \ge 0$ for all $t \in \mathbb{N}_0$, all $x_i^0 \in \mathbb{R}^n_+$ and all $i \in \underline{m}$. The terms γ_{ij} in (3.5) are as in (2.1) and are assumed to satisfy (A2)′. We note that the above framework permits the situation that D_k for $k \in \underline{m}$ is linear and corresponds to matrix multiplication, that

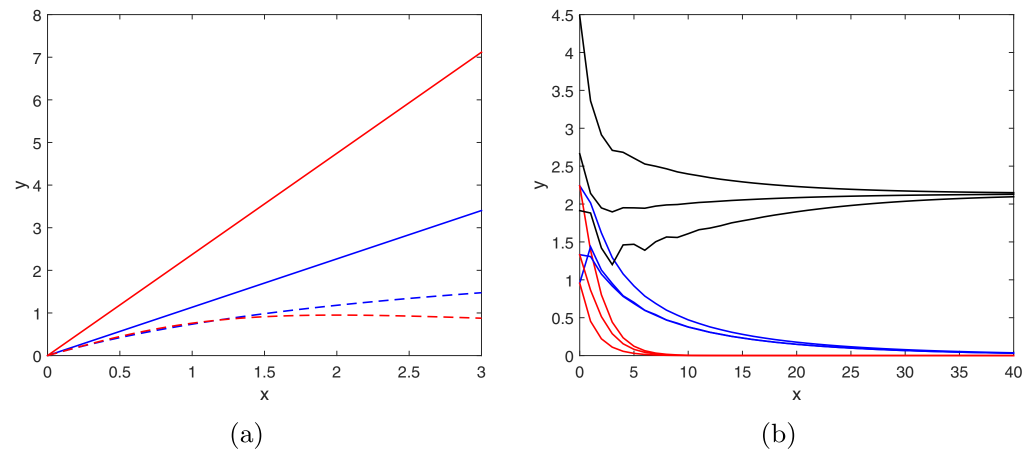

Fig. 3.2. Numerical simulations of the two-patch model with non-linear dynamics from Example 3.1. (a) Sector condition for F_1 (dashed blue) and F_2 (dashed red) curves. The straight lines have slopes $1/(C_1(I-A_1)^{-1}B_1)$ (blue) and $1/(C_2(I-A_2)^{-1}B_2)$ (red) (b) Norms of sample trajectories $\|x_i\|_1$ of the individual patch models (3.1) with model data 3.6 and $x=(x_1,x_2)$ of the dispersal model (3.5) from three (pseudo) random initial conditions. The blue, red and black curves correspond to patches one, two and the combined model, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is, $D_k(x) = D_k x$ for all $x \in \mathbb{R}^n_+$. In such a situation we shall abuse notation and use the symbol D_k to denote both the function and the matrix.

Example 3.1. We reconsider Example 2.2, but introduce density-dependent recruitment in both patches. Specifically, we consider

$$\left.\begin{aligned} A_1 &= \begin{bmatrix} 0 & 0 & 0 \\ 0.65 & 0 & 0 \\ 0 & 0.03 & 0.05 \end{bmatrix} \quad B_1 = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} \\ C_1 &= \begin{bmatrix} 0.06 & 1.16 & 3.29 \end{bmatrix} \\ A_2 &= \begin{bmatrix} 0 & 0 & 0 \\ 0.18 & 0.39 & 0 \\ 0 & 0.41 & 0.35 \end{bmatrix} \quad B_2 = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} \\ C_2 &= \begin{bmatrix} 0.41 & 0.02 & 0.03 \end{bmatrix} \end{aligned}\right\} \tag{3.6a}$$

with $F_1, F_2 : \mathbb{R}_+ \to \mathbb{R}_+$ defined by

$$F_1(w) = \frac{2.95w}{3+w} \quad \text{and} \quad F_2(w) = \frac{0.95w}{1+0.25w^2}. \tag{3.6b}$$

Note that $A_1 + B_1C_1$ and $A_2 + B_2C_2$ are equal to the matrices in (2.2). The solution of each of the patch models without dispersal (3.1) converges exponentially to zero, which may be established by checking that (3.2) and (3.4) hold for $i \in \{1, 2\}$. It is more readily seen graphically in Fig. 3.2 (a), by noting that the graphs of F_1 and F_2 are contained within the sector with slopes $\theta/(C_1(I-A_1)^{-1}B_1)$ and $\theta/(C_2(I-A_2)^{-1}B_2)$, respectively, for some $\theta < 1$.

Introducing the dispersal terms D_1 and D_2 as in (2.2), with $\gamma_{12} = \gamma_{21} = 0.95$ the combined model (3.5) exhibits DDG. Fig. 3.2 (b) plots sample state trajectories from both the individual patches (without dispersal) as well as the dispersal model (3.5). As expected, the state trajectories from the individual patches converge to zero, whereas the state trajectory of the dispersal model converges to a non-zero equilibrium. Since the functions F_1 and F_2 are bounded, it follows that for any initial conditions, first, the solutions of the two separate (declining) patches are bounded and, second, that the solution of the combined patch model (3.5) is also bounded. ♢

3.2. A necessary condition for dispersal driven growth

Our main result of this section provides a necessary condition for DDG to occur in the dispersal model (3.5). For ease of exposition, the proofs of all results in this section are relegated to the appendix.

Theorem 3.2. *Given the dispersal model (3.5), assume that $(A1)'$ and (B1)–(B3) hold. If there exists nonnegative vectors $q_i \in \mathbb{R}^p_+$, $r_i \in \mathbb{R}^\ell_+$ and strictly positive $\rho \in \mathbb{R}^n_+$ such that*

$$\rho^T A_i - \rho^T + q_i^T C_i \ll 0 \quad \text{and} \quad \rho^T B_i - r_i^T \ll 0 \quad i \in \underline{m}, \tag{3.7}$$

then the zero equilibrium of the dispersal model (3.5) is globally exponentially stable, for all functions F_i which satisfy

$$r_i^T F_i(y) \le q_i^T y \quad \forall\, y \in \mathbb{R}^p_+, \quad i \in \underline{m}, \tag{3.8}$$

for all dispersal functions $\{D_1, \dots, D_m\}$ and for all dispersal weightings (γ_{ij}). In other words, under these assumptions, DDG is not possible in (3.5).

Our next result demonstrates that the existence of a strictly positive ρ satisfying (3.7) — the key condition made in Theorem 3.2 — is also a necessary condition for ruling out DDG when the patch dynamics are assumed non-linear and dispersal is modelled multiplicatively.

Proposition 3.3. *Given the dispersal model*

$$\left.\begin{aligned} x_i(t+1) &= A_i\Big[\Theta_i(t)x_i(t) + \sum_{\substack{j=1\\ j\ne i}}^m \gamma_{ij}(t)(I-\Theta_j(t))x_j(t)\Big] \\ &\quad + B_iF_i\Big(C_i\Big[\Theta_i(t)x_i(t) + \sum_{\substack{j=1\\ j\ne i}}^m \gamma_{ij}(t)(I-\Theta_j(t))x_j(t)\Big]\Big) \\ x_i(0) &= x_i^0,\ t \in \mathbb{N}_0,\ i \in \underline{m}, \end{aligned}\right\} \tag{3.9}$$

for $m \in \mathbb{N}$, assume that (B1), (B2), $(A2)'$ and

$(B3)'$ $\Theta_i(t) \in \mathbb{R}^{n\times n}_+$ and $\Theta_i(t)$ is diagonal with diagonal entries taking values in $[0, 1]$ for every $i \in \underline{m}$ and $t \in \mathbb{N}_0$

hold. If there exists nonnegative vectors $q_i \in \mathbb{R}^p_+$, $r_i \in \mathbb{R}^\ell_+$ and strictly positive $\rho \in \mathbb{R}^n_+$ such that (3.7) holds, then the zero equilibrium of the dispersal model (3.9) is globally exponentially stable, for all functions F_i which satisfy (3.8), for all dispersal functions

$\{\theta_1, \ldots, \theta_m\}$ and for all dispersal weightings (γ_{ij}). In other words, under these assumptions, DDG is not possible in (3.9).

We conclude this section with some remarks.

Remark 3.4.

(a) Given model data (A_i, B_i, C_i) and $q_i \in \mathbb{R}^p_+$, $r_i \in \mathbb{R}^\ell_+$, checking whether there exists a strictly positive $\rho \in \mathbb{R}^n_+$ such that (3.7) holds may be formulated as a linear program, and is thus readily implemented numerically.

(b) The inferences which may be drawn from Theorem 3.2 parallel those which follow from the earlier result, Theorem 2.6, which treats the linear case. For example, DDG is not possible in (3.5) when each patch has scalar dynamics (meaning $n = \ell = p = 1$) and satisfies (3.2) and (3.3), cf. statement (1) of Corollary 2.7. Recall that these assumptions imply that the zero equilibrium of each patch (without dispersal) is GES and in the scalar case means that there exists (scalar) $\rho_i > 0$ such that

$$\rho_i a_i - \rho_i + q_i c_i < 0 \quad \text{and} \quad \rho_i b_i - r_i < 0 \quad \forall\, i \in \underline{m}\,. \tag{3.10}$$

Note that the first inequality implies that $a_i < 1$ for all $i \in \underline{m}$. By taking

$$\rho := \min_{j \in \underline{m}} \frac{q_j c_j}{1 - a_j} + \varepsilon\,,$$

for $\varepsilon > 0$ sufficiently small, it may be proven from (3.10) that ρ satisfies *all* the inequalities

$$\rho a_i - \rho + q_i c_i < 0 \quad \text{and} \quad \rho b_i - r_i < 0 \quad \forall\, i \in \underline{m}\,.$$

and Theorem 3.2 thus applies.

(c) The analogous version of statement (3) of Corollary 2.7 applies to the dispersal model (3.5). Namely, the patch models (A_i, B_i, C_i), together with r_i and q_i that constrain the nonlinear terms F_i, must be sufficiently distinct — in the sense that they do not admit a strictly positive $\rho \in \mathbb{R}^n_+$ satisfying (3.7) — for DDG to be possible. □

4. Dispersal driven growth in continuous-time models

The penultimate section demonstrates that versions of the discrete-time results stated and proven in Sections 2 and 3 translate to their continuous-time analogues. The proofs of Theorems 4.2 and 4.3 appear in the Appendix. The interpretation of these results is similar to that of their discrete-time counterparts, and thus commentary is kept to a minimum. One purpose of this short section is to substantiate the claim that, at least theoretically, our test for DDG in terms of a non-existence of a CLLF is not an artefact of the assumed discrete-time modelling framework. We do note that discrete-time models seem more prevalent in ecology than their continuous-time counterparts. However, as an example of a positive dynamical system, the dispersal model (4.1) may have applications outside of ecology, say, in models for transport, logistics, communications or flows on networks (Haddad et al., 2010).

The continuous-time version of the linear patch model (2.1) is:

$$\dot{x}_i(t) = A_i x_i(t) - D_i x_i(t) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij} D_j x_j(t), \quad x_i(0) = x_i^0,$$
$$t \in \mathbb{R}_+, \quad i \in \underline{m}, \tag{4.1}$$

where $m \in \mathbb{N}$. We here assume that:

(C1) A_i and $A_i - D_i$ are Metzler and $D_i \geq 0$ for every $i \in \underline{m}$;
(C2) $\gamma_{ij} \in [0, 1]$ and $\sum_{\substack{k=1\\ k\neq j}}^m \gamma_{kj} \in [0, 1]$, for every $i, j \in \underline{m}$;
(C3) $\alpha(A_i) < 0$, for every $i \in \underline{m}$.

Recall that a square matrix M is called Metzler if every off-diagonal entry is nonnegative (see, for example, (Berman and Plemmons, 1994, Ch. 6)). Further, $\alpha(M)$ denotes the spectral abscissa of M, given by

$$\alpha(M) := \max\{\mathrm{Re}\,\lambda \;:\; \lambda \in \sigma(M)\}\,.$$

Metzler matrices go by the terms essentially non-negative (Berman et al., 1989, p. 146) or quasi positive (Smith, 1995, p. 60), as well. In a dynamical systems context, they are the continuous-time analogue of nonnegative matrices. The following well-known result (see, for example, Smith (1995, Section 3.1)) demonstrates that the Metzler property characterises linear flows which leave the nonnegative orthant invariant: a matrix $M \in \mathbb{R}^{n\times n}$ is Metzler if, and only if, $e^{Mt} > 0$ for all $t \geq 0$.

We mention that assumption (C1) is satisfied if A_i is Metzler and D_i is diagonal with nonnegative diagonal entries, for each $i \in \underline{m}$. In this case the diagonal entries of D_i may be arbitrarily large, as they correspond to dispersal rates, not proportions. Assumption (C3) is the continuous-time version of (A3) and implies that without dispersal (that is, $D_i = 0$ for all $i \in \underline{m}$), the solution x_i of the dynamics of i-th patch satisfies

$$\dot{x}_i(t) = A_i x_i(t) \quad \Rightarrow \quad x_i(t) = e^{A_i t} x_i^0 \to 0 \quad \text{as } t \to \infty \quad \forall\, x_i^0 \in \mathbb{R}^n_+\,.$$

Definition 4.1. A set of Metzler matrices $\{A_1, \ldots, A_m\} \subseteq \mathbb{R}^{n\times n}_+$ admits a common linear Lyapunov function (CLLF) if there exists a strictly positive $v \in \mathbb{R}^n_+$ and $a > 0$ such that

$$v^T A_i \leq -a v^T, \quad i \in \underline{m}\,. \tag{4.2}$$

Paralleling Definition 2.5 and the comments afterwards, if the set of Metzler matrices $\{A_1, \ldots, A_m\}$ admits a CLLF in the sense of Definition 4.1, then assumption (C3) holds. This claim follow from, for example Berman and Plemmons (1994, Theorem 6.2.3, characterisation I_{27}), noting that P is a Metzler matrix with $\alpha(P) < 0$ if, and only if, $-P$ is a non-singular M-matrix. The converse is not true in general.

Theorem 4.2. *If the set of Metzler matrices $\{A_1, \ldots, A_m\}$ admits a common linear Lyapunov function, then the zero equilibrium of the dispersal model (4.1) is globally exponentially stable, for all dispersal matrices $\{D_1, \ldots, D_m\}$ and for all weightings (γ_{ij}) which satisfy assumptions (C1)–(C2). Consequently, that $\{A_1, \ldots, A_m\}$ does not admit a CLLF is a necessary condition for DDG to occur.*

The analogous versions of Corollaries 2.7, 2.11 and 2.12 hold in the continuous-time case, mutatis mutandis. For the sake of brevity, we do not give formal statements. The case of dispersal acting multiplicatively, viz. Corollary 2.14, *does not* have a natural continuous-time analogue, as here the right hand side of (4.1) describes rates of change of the x_i, not the actual change of x_i (which as a nonnegative quantity, is necessarily a proportion).

We comment that Fornasini and Valcher (2010); Knorn et al. (2009) contain checkable characterisations for a set of Metzler matrices to admit a CLLF. Alternatively, testing for a CLLF in practice may be formulated as a linear program, analogously to as proposed in Example 2.9.

To accommodate dispersal between density-dependent (nonlinear) patch dynamics, modelled in continuous-time, we consider:

$$\dot{x}_i(t) = A_i x_i(t) + B_i F_i(C_i x_i(t)) - D_i x_i(t) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(t) D_j x_j(t),$$
$$x_i(0) = x_i^0, \; t \in \mathbb{R}_+, \; i \in \underline{m}, \tag{4.3}$$

where $m \in \mathbb{N}$ and, we additionally assume that

(C4) $F_i : \mathbb{R}^p_+ \to \mathbb{R}^\ell_+$ is locally Lipschitz continuous and there exists $R_i > 0$ such that

$$\|F_i(y)\| \le R_i \|y_i\| \quad \forall\, y \in \mathbb{R}^p_+,\ \forall\, i \in \underline{m}.$$

From standard theory of differential equations, the assumptions (C1)–(C4) imply that for all $x_i^0 \in \mathbb{R}^n_+$, the differential equation (4.3) has a unique solution defined for all $t \ge 0$ see, for example, Logemann and Ryan (2014, Proposition 4.24).

Theorem 4.3. *Given the dispersal model (4.3), assume that (C1), (C2) and (C4) hold. If there exists nonnegative vectors $q_i \in \mathbb{R}^p_+$, $r_i \in \mathbb{R}^\ell_+$ and strictly positive $\rho \in \mathbb{R}^n_+$ such that*

$$\rho^T A_i + q_i^T C_i \ll 0 \quad \text{and} \quad \rho^T B_i - r_i^T \ll 0 \quad \forall\, i \in \underline{m}\,, \tag{4.4}$$

then the zero equilibrium of the dispersal model (4.3) is globally exponentially stable, for all functions F_i which satisfy (3.8), for all dispersal matrices $\{D_1, \dots, D_m\}$ and for all dispersal weightings (γ_{ij}). In other words, under these assumptions, DDG is not possible in (4.3).

5. Discussion

Models for structured populations with a discrete spatial (patch) structure coupled via dispersal have been considered. We have focussed on the situation wherein each patch is a sink, but the inclusion of dispersal between patches leads to overall population growth — so-called dispersal driven growth. Such a phenomenon may occur, at least theoretically, in the absence of either a source patch or contribution from external immigration. Our results supplement the existing body of literature on population persistence and, for example, are potentially of interest and utility to those both looking to eradicate, or control, an invasive population, or conserve another. We have shown that for the classes of models considered, if the terms modelling the dynamics on each patch admit a common linear Lyapunov function, then the zero equilibrium is globally asymptotically stable, irrespective of the dispersal terms, which thus rules out DDG. In other words, we have derived a necessary condition for DDG to occur.

The first class of models considered were discrete-time and linear (hence specified by nonnegative matrices), Section 2, and our main results are formulated as Theorem 2.6 and Corollary 2.7. Given a set of nonnegative matrices, a checkable characterisation exists for testing whether the set admits a CLLF, see Example 2.9, and linear programming may also readily be implemented. Several extensions were considered to, for example, time-varying, delayed or non-linear dispersal and worked examples have been presented. Sections 3 and 4 considered classes of models with nonlinear patch dynamics and in continuous time, respectively. Qualitatively, the same results as in Section 2 were obtained — existence of a CLLF, interpreted appropriately, rules out the possibility of DDG.

We conclude the present paper by considering some of the biological and mathematical implications of Corollary 2.7. Statements (2)–(4) of Corollary 2.7 demonstrate that for DDG to be possible, (at least some of) the matrices A_i must be distinct from one another. Noting that the left eigenvector of a nonnegative matrix A corresponding to the spectral radius $r(A)$ satisfies $v^T A = r(A) v^T$, the definition of a CLLF for a set $\{A_1, \dots, A_m\}$ is roughly similar to the assertion that the matrices A_i have a common left eigenvector, which is the case if the A_i all commute, for instance. Recall that in our applied context the A_i seek to capture the biological processes occurring on each patch — which are affected by local factors such as environmental quality, availability of and access to food, risk of predation or disease, and so on. For such matrix projection models, the left eigenvector v^T (unique once a scaling is fixed) corresponding to $r(A)$ is often called the reproductive vector, as it contains the reproductive values (as in Fisher, 1958) of each stage-class (Goodman, 1968). The claim that the A_i must be sufficiently distinct supports the intuition that connecting multiple versions of the same patch cannot lead to asymptotic growth, *when each patch* is assumed to be asymptotically declining without dispersal.

Further, statements (4) and (5) of Corollary 2.7 indicate that for DDG to be possible some patches must have dynamics which exhibit transient growth, that is, certain stage-classes must cause short-term population growth. These conclusions support the intuition that DDG is likely to occur when distinct stage-classes of a population amplify short-term in distinct patches. The cumulative effect of combining these “boomy” patches is overall growth, or DDG. This assertion complements the findings of Elragig and Townley (2012) or Neubert et al. (2002), there in the context of Turing Instability in reaction-diffusion equations. We emphasise that the converse of the above remarks *need not* hold (cf. statement (6) of Corollary 2.7), meaning that the set of matrices $\{A_1, \dots, A_m\}$ could exhibit wide variation or marked transient growth, yet the combined dispersal model (2.1) *still does not* exhibit DDG for some γ_{ij} and $\{D_1, \dots, D_m\}$ parameters. As we discussed at the end of Section 2.2, determining when DDG does occur in terms of the model parameters is analytically intractable, in general. We reiterate here that the value of Theorem 2.6 and its extensions is that a readily checkable condition is available for “ruling out” DDG, not “ruling it in”.

Finally, statement (1) of Corollary 2.7 makes a rather different claim to the others, which may be rationalised as follows. For scalar, linear dynamical systems $x(t+1) = a x(t)$ with $a > 0$, there is no distinction between transient and asymptotic behaviour — the solution is given by $x(t) = a^t x(0)$ which either grows or shrinks (discarding $a = 1$ or $x(0) = 0$) at every time-step from $t = 0$, dependent on whether $a > 1$ or $a < 1$, respectively. Since we have already commented that some transient growth is necessary for DDG to occur — scalar models shall never exhibit DDG by our insistence that $a < 1$ — our imposed asymptotic decline. By way of contrast, a matrix A may have both $r(A) < 1$ but $\|A\|_1$ arbitrarily large, in which case the solution x of $x(t+1) = Ax(t)$ may grow in norm short-term, before eventually declining. Thus scalar models do not capture the richness of transient dynamics required to see DDG and, biologically, do not capture the different vital rates associated with different developmental-stage classes.

Appendix A. Remaining proofs of stated results

Proof of Theorem 3.2. We note that the condition (3.7) implies that for each $i \in \underline{m}$

$$\rho^T A_i - \rho^T \le \rho^T A_i - \rho^T + q_i^T C_i \ll 0 \quad \Rightarrow \quad \rho^T A_i \ll \rho^T\,,$$

and hence assumption (A3) holds by, for example, Krasnosel'skij et al. (1989, Lemma 16.1). Let $x := (x_1, \dots, x_m)$ denote the solution of (3.5). We note that assumptions (B1)–(B3) ensure that $x_i(t) \ge 0$ for each $t \in \mathbb{N}_0$ and $i \in \underline{m}$ and thus $x(t) \in \mathbb{R}^{nm}_+$ for each $t \in \mathbb{N}_0$.

Choose $\mu > 1$ such that

$$r(\mu A_i) = \mu r(A_i) < 1 \quad \forall\, i \in \underline{m}\,, \tag{A.1}$$

and

$$\rho^T \mu A_i - \rho^T + q^T C_i \le 0 \quad \text{and} \quad \rho^T \mu B_i - r^T \le 0 \quad \forall\, i \in \underline{m}\,, \tag{A.2}$$

which is possible by (A3) and (3.7). Define $w := (w_1, \ldots, w_m)$ and W by

$$w_i(t) := \mu^t x_i(t) \quad i \in \underline{m},\ t \in \mathbb{N}_0 \quad \text{and} \quad W : \mathbb{R}^{nm} \to \mathbb{R}_+,$$
$$W((z_1, \ldots, z_m)) := \sum_{j=1}^{m} \rho^T z_j.$$

A routine calculation using (3.5) shows that w_i has dynamics given by

$$w_i(t+1) = \mu A_i w_i(t) + \mu B_i \mu^t F_i(\mu^{-t} C_i w_i(t)) - \mu^t D_i(\mu^{-t} w_i(t)) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij} \mu^t D_j(\mu^{-t} w_j(t)),\ t \in \mathbb{N}_0,\ i \in \underline{m}, \tag{A.3}$$

Applying (3.8) to $y = \mu^{-\tau}\xi$ for $\xi \in \mathbb{R}^p_+$ and $\tau \in \mathbb{N}_0$, and multiplying both sides by μ^τ yields

$$\mu^\tau r_i^T F_i(\mu^{-\tau}\xi) \le \mu^\tau \cdot q_i^T \left(\mu^{-\tau}\xi\right) = q_i^T \xi \quad \forall\, \xi \in \mathbb{R}^p_+ \quad \forall\, i \in \underline{m}. \tag{A.4}$$

For $t \in \mathbb{N}_0$, we now estimate $W(w)$ using (A.3) (suppressing the argument t of w for clarity)

$$\begin{aligned} W(w(t+1)) &= \sum_{i=1}^{m} \rho^T w_i(t+1) \\ &= \sum_{i=1}^{m} \rho^T \Big[\mu A_i w_i + \mu B_i \mu^t F_i(\mu^{-t} C_i w_i) - \mu^t D_i(\mu^{-t} w_i) \\ &\quad + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij} \mu^t D_j(\mu^{-t} w_j) \Big] \\ &\le \sum_{i=1}^{m} \rho^T w_i - q_i^T C_i w_i + r_i^T \mu^t F_i(\mu^{-t} C_i w_i) \\ &\quad - \sum_{i=1}^{m} \mu^t \rho^T D_i(\mu^{-t} w_i) \\ &\quad + \sum_{j=1}^{m} \Big(\sum_{\substack{i=1\\ i\neq j}}^{m} \gamma_{ij} \Big) \mu^t \rho^T D_i(\mu^{-t} w_i) \qquad \text{by (A.2),} \\ &\le W(w(t)) + \sum_{i=1}^{m} -q_i^T C_i w_i + r_i^T \mu^t F_i(\mu^{-t} C_i w_i) \\ &\quad \text{by (A2)}', \\ &\le W(w(t)), \end{aligned} \tag{A.5}$$

where in the last estimate we invoked (A.4). We conclude from (A.5) that $W(w)$ is bounded, specifically, that

$$0 \le W(w(t)) \le W(x^0) \quad \forall\, t \in \mathbb{N}_0.$$

Since ρ is strictly positive, the above bound implies that w is bounded, meaning there exists $M > 0$ such that

$$\|w(t)\| \le M\|x^0\| \quad \forall\, t \in \mathbb{N}_0. \tag{A.6}$$

Inserting the definition of w into (A.6), we see that

$$\|x(t)\| \le M\mu^{-t}\|x^0\| \to 0 \quad \text{as } t \to \infty,$$

which completes the proof. □

Proof of Proposition 3.3. Define μ, w and W as in the proof of Theorem 3.2. A routine calculation using (3.9) shows that w satisfies

$$\begin{aligned} w_i(t+1) &= \mu A_i \Big[\Theta_i(t) w_i(t) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(t)(I - \Theta_j(t)) w_j(t) \Big] \\ &\quad + \mu B_i \mu^t F_i \Big(\mu^{-t} C_i \Big[\Theta_i(t) w_i(t) \\ &\quad + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(t)(I - \Theta_j(t)) w_j(t) \Big] \Big) \quad t \in \mathbb{N}_0. \end{aligned} \tag{A.7}$$

For $t \in \mathbb{N}_0$, we now estimate using (A.7) (suppressing the argument t for clarity)

$$\begin{aligned} W(w(t+1)) &= \sum_{i=1}^{m} \rho^T w_i(t+1) \\ &= \sum_{i=1}^{m} \rho^T \Big\{ \mu A_i \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \\ &\quad + \mu B_i \mu^t F_i \Big(\mu^{-t} C_i \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \Big) \Big\} \\ &\le \sum_{i=1}^{m} \big(\rho^T - q_i^T C_i \big) \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \\ &\quad + r_i^T \mu^t F_i \Big(\mu^{-t} C_i \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \Big) \\ &\quad \text{by (3.7),} \\ &\le \sum_{i=1}^{m} \big(\rho^T - q_i^T C_i \big) \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \\ &\quad + q_i^T C_i \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \quad \text{by (A.4),} \\ &= \sum_{i=1}^{m} \rho^T \Big[\Theta_i w_i + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij}(I - \Theta_j) w_j \Big] \\ &= \sum_{i=1}^{m} \rho^T \Theta_i w_i + \sum_{j=1}^{m} \Big(\sum_{\substack{i=1\\ i\neq j}}^{m} \gamma_{ij} \Big) \rho^T (I - \Theta_j) w_j \\ &\le \sum_{i=1}^{m} \rho^T w_i \quad \text{by A2}' \\ &= W(w(t)). \end{aligned} \tag{A.8}$$

From (A.8) we infer that w is bounded, and hence the final part of the proof mirrors that of Theorem 3.2. □

Proof of Theorem 4.2. Let $x = (x_1, \ldots, x_m)$ denote the solution of (4.1) and define W as in (2.8). For $t \ge 0$, a calculation using (4.1), (4.2) and assumption (C2) shows that

$$\begin{aligned} \frac{d}{dt} W(x(t)) &= \sum_{i=1}^{m} v^T \dot{x}_i(t) \\ &= \sum_{i=1}^{j} v^T \Big[A_i x_i(t) - D_i x_i(t) + \sum_{\substack{j=1\\ j\neq i}}^{m} \gamma_{ij} D_j x_j(t) \Big] \end{aligned}$$

$$\leq \sum_{i=1}^{m} v^T A_i x_i(t) \leq -a \sum_{i=1}^{m} v^T x_i(t)$$
$$= -aW(x(t)),$$

whence

$$0 \leq W(x(t)) \leq \mathrm{e}^{-at} W(x^0) \quad \forall\, t \geq 0\,. \tag{A.9}$$

The inequalities in (A.9) prove that $W(x(t)) \to 0$ as $t \to \infty$, and hence $x(t) \to 0$ as $t \to \infty$ because v is strictly positive and $x_i(t) \geq 0$ for all $t \geq 0$ and each $i \in \underline{m}$. □

Proof of Theorem 4.3. We begin by noting that the first condition in (4.4) implies that for each $i \in \underline{m}$

$$\rho^T A_i \leq \rho^T A_i + q_i^T C_i \ll 0 \quad \Rightarrow \quad \rho^T A_i \ll 0\,,$$

and so property (C3) holds (see the comment after Definition 4.1). Let $x := (x_1, \ldots, x_m)$ denote the solution of (4.3). We note that assumptions (C1), (C2) and (C4) ensure that $x_i(t) \geq 0$ for each $t \in \mathbb{R}_+$ and $i \in \underline{m}$ and thus $x(t) \in \mathbb{R}_+^{nm}$ for all $t \in \mathbb{R}_+$.

Choose $\gamma > 0$ such that

$$\alpha(A_i + \gamma I) = \alpha(A_i) + \gamma < 0 \quad \forall\, i \in \underline{m}\,, \tag{A.10}$$

and

$$\rho^T (A_i + \gamma I) + q^T C_i \leq 0 \quad \text{and} \quad \rho^T B_i - r^T \leq 0 \quad \forall\, i \in \underline{m}\,, \tag{A.11}$$

which is possible by (C3) and (4.4). Define $w := (w_1, \ldots, w_m)$ and W by

$$w_i(t) := \mathrm{e}^{\gamma t} x_i(t) \quad i \in \underline{m},\ t \in \mathbb{R}_+ \quad \text{and} \quad W : \mathbb{R}^{nm} \to \mathbb{R}_+,$$
$$W((z_1, \ldots, z_m)) := \sum_{j=1}^{m} \rho^T z_j\,.$$

A routine calculation using (4.3) shows that w_i has dynamics given by

$$\dot{w}_i(t) = (A_i + \gamma I) w_i(t) + B_i \mathrm{e}^{\gamma t} F_i(\mathrm{e}^{-\gamma t} C_i w_i(t)) - D_i w_i(t)$$
$$+ \sum_{\substack{j=1 \\ j \neq i}}^{m} \gamma_{ij} D_j w_j(t),\ t \in \mathbb{R}_+,\ i \in \underline{m}\,, \tag{A.12}$$

Applying (3.8) to $y = \mathrm{e}^{-\gamma\tau}\xi$ for $\xi \in \mathbb{R}_+^p$ and $\tau \in \mathbb{R}_+$, and multiplying both sides by $\mathrm{e}^{\gamma\tau}$ yields

$$\mathrm{e}^{\gamma\tau} r^T F_i(\mathrm{e}^{-\gamma\tau}\xi) \leq \mathrm{e}^{\gamma\tau} \cdot q^T\left(\mathrm{e}^{-\gamma\tau}\xi\right) = q^T \xi \quad \forall\, \xi \in \mathbb{R}_+^p \quad \forall\, i \in \underline{m}\,. \tag{A.13}$$

We now estimate $t \mapsto \frac{d}{dt} W(w(t))$ using (A.12) for $t \geq 0$

$$\frac{d}{dt} W(w(t)) = \sum_{i=1}^{m} \rho^T \dot{w}_i(t)$$
$$= \sum_{i=1}^{m} \rho^T \Big[(A_i + \gamma I) w_i(t) + B_i \mathrm{e}^{\gamma t} F_i(\mathrm{e}^{-\gamma t} C_i w_i(t))$$
$$- D_i w_i(t) + \sum_{\substack{j=1 \\ j \neq i}}^{m} \gamma_{ij} D_j w_j(t) \Big]$$
$$\leq \sum_{i=1}^{m} \rho^T \Big[(A_i + \gamma I) w_i(t) + B_i \mathrm{e}^{\gamma t} F_i(\mathrm{e}^{-\gamma t} C_i w_i(t)) \Big] \quad \text{by (C2)}$$
$$\leq \sum_{i=1}^{m} \Big[-q_i^T C_i w_i + r_i^T \mathrm{e}^{\gamma t} F_i(\mathrm{e}^{-\gamma t} C_i w_i) \Big] \quad \text{by(A.11)}$$
$$\leq 0, \tag{A.14}$$

where in the last estimate we invoked (A.13). We conclude from (A.14) that $W(w)$ is bounded, specifically, that

$$0 \leq W(w(t)) \leq W(x^0) \quad \forall\, t \in \mathbb{R}_+\,.$$

Since ρ is strictly positive, the above bound implies that w is bounded, meaning there exists $M > 0$ such that

$$\|w(t)\| \leq M \|x^0\| \quad \forall\, t \in \mathbb{R}_+\,. \tag{A.15}$$

Inserting the definition of w into (A.15), we see that $x(t) \to 0$ as $t \to \infty$, which completes the proof. □

References

Berman, A., Neumann, M., Stern, R.J., 1989. Nonnegative Matrices in Dynamic Systems. John Wiley & Sons Inc., New York.
Berman, A., Plemmons, R.J., 1994. Nonnegative Matrices in the Mathematical Sciences. SIAM, Philadephia.
Beverton, R., Holt, S., 1957. On the dynamics of exploited fish populations. London: Ministry of Agriculture Fisheries and Food. Vol. 2 of Fisheries Investigation Series.
Briat, C., 2013. Robust stability and stabilization of uncertain linear positive systems via integral linear constraints: L_1-gain and L_∞-gain characterization. Int. J. Robust Nonlinear Control 23, 1932–1954.
Caswell, H., 2001. Matrix Population Models : Construction, Analysis, and Interpretation. Sinauer Associates,Sunderland.
Caswell, H., 2007. Sensitivity analysis of transient population dynamics. Ecol. Lett. 10, 1–15.
Courchamp, F., Berec, L., Gascoigne, J., 2008. Allee effects in ecology and conservation. Environ. Conserv. 36, 80–85.
Davis, J.L.D., Levin, L.A., 2002. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin clinocottus analis. Mar. Ecol. Prog. Ser. 234, 229–246.
Demetrius, L., 1969. The sensitivity of population growth rate to pertubations in the life cycle components. Math. Biosci. 4, 129–136.
Eager, E.A., 2016. Modelling and analysis of population dynamics using lur'e systems accounting for competition from adult conspecifics. Lett. Biomath. 3, 41–58.
Eager, E.A., Guiver, C., Hodgson, D., Rebarber, R., Stott, I., Townley, S., 2014a. Bounds on the dynamics of sink populations with noisy immigration. Theor. Popul. Biol. 92, 88–96.
Eager, E.A., Rebarber, R., Tenhumberg, B., 2014b. Global asymptotic stability of plant-seed bank models. J. Math. Biol. 69, 1–37.
Elragig, A., Townley, S., 2012. A new necessary condition for turing instabilities. Math. Biosci. 239, 131–138.
Ezard, T., Bullock, J., Dalgleish, H., Millon, A., Pelletier, F., Ozgul, A., Koons, D., 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. J. Appl. Ecol. 47, 515–523.
Fisher, R.A., 1958. The Genetical Theory of Natural Selection. Oxford University Press, Oxford.
Fornasini, E., Valcher, M.E., 2010. Linear copositive lyapunov functions for continuous-time positive switched systems. IEEE Trans. Autom. Control 55, 1933–1937.
Fornasini, E., Valcher, M.E., 2012. Stability and stabilizability criteria for discrete–time positive switched systems. IEEE Trans. Autom. Control 57, 1208–1221.
Franco, D., Logemann, H., Perán, J., 2014. Global stability of an age-structured population model. Syst. Control Lett. 65, 30–36.
Gonzalez, A., Holt, R.D., 2002. The inflationary effects of environmental fluctuations in source–sink systems. Proc. Natl. Acad. Sci. U.S.A. 99, 14872–14877.
Goodman, L.A., 1968. An elementary approach to the population projection-matrix, to the population reproductive value, and to related topics in the mathematical theory of population growth. Demography 5, 382–409.
Haddad, W.M., Chellaboina, V., 2005. Stability and dissipativity theory for nonnegative dynamical systems: a unified analysis framework for biological and physiological systems. Nonlinear Anal. Real World Appl. 6, 35–65.
Haddad, W.M., Chellaboina, V., Hui, Q., 2010. Nonnegative and Compartmental Dynamical Systems. Princeton University Press, Princeton.
Haddad, W.M., Chellaboina, V.S., August, E., 2003. Stability and dissipativity theory for discrete-time non-negative and compartmental dynamical systems. Int. J. Control 76, 1845–1861.
Hastings, A., 2004. Transients: the key to long-term ecological understanding? Trends Ecol. Evol. 19, 39–45.
Hinrichsen, D., Plischke, E., 2007. Robust stability and transient behaviour of positive linear systems. Vietnam J. Math. 35, 429–462.
Hinrichsen, D., Pritchard, A.J., 1986a. Stability radii of linear systems. Syst. Control Lett. 7, 1–10.
Hinrichsen, D., Pritchard, A.J., 1986b. Stability radius for structured perturbations and the algebraic riccati equation. Syst. Control Lett. 8, 105–113.
Hinrichsen, D., Pritchard, A.J., 2005. Mathematical Systems Theory I. Springer-Verlag, Berlin.
Hinrichsen, D., Son, N.K., 1998. Stability radii of positive discrete-time systems under affine parameter perturbations. Int. J. Robust Nonlinear Control 8, 1169–1188.
Hodgson, D., Townley, S., 2004. Methodological insight: linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. J. Appl. Ecol. 41, 1155–1161.

Hodgson, D., Townley, S., McCarthy, D., 2006. Robustness: predicting the effects of life history perturbations on stage-structured population dynamics. Theor. Popul. Biol. 70, 214–224.
Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398.
Holt, R.D., Barfield, M., Gonzalez, A., 2003. Impacts of environmental variability in open populations and communities:nflationin sink environments. Theor. Popul. Biol. 64, 315–330.
Hunter, C.M., Caswell, H., 2005. The use of the vec-permutation matrix in spatial matrix population models. Ecol. Model. 188, 15–21.
Jayawardhana, B., Logemann, H., Ryan, E., 2011. The circle criterion and input-to-state stability: new perspectives on a classical result. IEEE Control Syst. Mag. 31, 32–67.
Kato, T., 1995. Perturbation theory for linear operators. Classics in Mathematics. Springer-Verlag, Berlin.
Knorn, F., Mason, O., Shorten, R., 2009. On linear co-positive lyapunov functions for sets of linear positive systems. Automatica 45, 1943–1947.
Kottas, K.L., 2012. Life History and Modeling of an Endangered Plant, Penstemon Haydenii. University of Nebraska, Lincoln, US Ph.d. thesis.
Krasnosel'skij, M.A., Lifshits, J.A., Sobolev, A.V., 1989. Positive Linear Systems: The Method of Positive Operators. Heldermann Verlag, Berlin.
de Kroon, H., Plaisier, A., van Groenendael, J., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67, 1427–1431.
Liberzon, D., Morse, A.S., 1999. Basic problems in stability and design of switched systems. IEEE Control Syst. Mag. 19, 59–70.
Liberzon, M., 2006. Essays on the absolute stability theory. Autom. Remote Control 67, 1610–1644.
Lin, H., Antsaklis, P.J., 2009. Stability and stabilizability of switched linear systems: a survey of recent results. IEEE Trans. Autom. Control 54, 308–322.
Logemann, H., Ryan, E.P., 2014. Ordinary Differential Equations. Springer, London.
Lubben, J., Boeckner, D., Rebarber, R., Townley, S., Tenhumberg, B., 2009. Parameterizing the growth-decline boundary for uncertain population projection models. Theor. Popul. Biol. 75, 85–97.
Matthews, D.P., Gonzalez, A., 2007. The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations. Ecology 88, 2848–2856.
Murray, J., 1982. Parameter space for turing instability in reaction diffusion mechanisms: a comparison of models. J. Theor. Biol. 98, 143–163.
Murray, J.D., 2002. Mathematical Biology. I, 3rd ed. Springer-Verlag, New York.
Neubert, M.G., Caswell, H., Murray, J., 2002. Transient dynamics and pattern formation: reactivity is necessary for turing instabilities. Math. Biosci. 175, 1–11.
Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.
Rebarber, R., Tenhumberg, B., Townley, S., 2011. Global asymptotic stability of density dependent integral population projection models. Theor. Popul. Biol. 81, 81–87.
MATLAB and Statistics Toolbox Release 2014a. The MathWorks, Inc., Natick, Massachusetts, United States.
Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Board Can. 11, 559–623.
Roy, M., Holt, R.D., Barfield, M., 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. Am. Nat. 166, 246–261.
Schreiber, S.J., 2012. Persistence for stochastic difference equations: a mini-review. J. Difference Equ. Appl. 18, 1381–1403.
Smith, H.L., 1995. Monotone Dynamical Systems. American Mathematical Society, Providence.
Smith, H.L., Thieme, H.R., 2011. Dynamical Systems and Population Persistence. American Mathematical Society, Providence.
Smith, H.L., Thieme, H.R., 2013. Persistence and global stability for a class of discrete time structured population models. Discrete Contin. Dyn. Syst. 33, 4627–4646.
Son, N.K., Hinrichsen, D., 1996. Robust stability of positive continuous time systems. Numer. Funct. Anal. Optim. 17, 649–659.
Sontag, E.D., 1998. Mathematical Control Theory, 2nd ed. Springer-Verlag, New York.
Stewart, G.W., Sun, J.G., 1990. Matrix Perturbation Theory(Computer Science and Scientific Computing). Academic Press, Inc., Boston.
Stott, I., Townley, S., Carslake, D., Hodgson, D., 2010. On reducibility and ergodicity of population projection matrix models. Methods Ecol. Evol. 1, 242–252.
Stott, I., Townley, S., Hodgson, D.J., 2011. A framework for studying transient dynamics of population projection matrix models. Ecol. Lett. 14, 959–970.
Townley, S., Rebarber, R., Tenhumberg, B., 2012. Feedback control systems analysis of density dependent population dynamics. Syst. Control Lett. 61, 309–315.
Turing, A.M., 1952. The chemical basis of morphogenesis. Philos. Trans. Roy. Soc. London Ser. A 237, 37–72.
Vidyasagar, M., 2002. Nonlinear Systems Analysis. SIAM, Philadelphia.
Wilkinson, J.H., 1988. The algebraic eigenvalue problem. Monographs on Numerical Analysis. The Clarendon Press, Oxford University Press.
Wootton, J.T., Bell, D.A., 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. Ecol. Appl. 307–321.