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

A B S T R A C T

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

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

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

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.