



# Spreading speeds for plant populations in landscapes with low environmental variation



Mark A. Gilbert<sup>a,b,\*</sup>, Eamonn A. Gaffney<sup>a</sup>, James M. Bullock<sup>b</sup>, Steven M. White<sup>a,b</sup>

<sup>a</sup> Wolfson Centre for Mathematical Biology, Mathematical Institute, Radcliffe Observatory Quarter, Woodstock Road, Oxford, Oxfordshire OX2 6GG, UK

<sup>b</sup> Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire OX10 8BB, UK

## HIGHLIGHTS

- We develop integrodifference equations for systems with low environmental variation.
- We use analytical methods to compare spread rates with the homogeneous model.
- The spread rates of the spatially varying model and its homogenisation are very close.
- This justifies the approximation of these landscapes with the homogeneous model.
- For cases requiring greater accuracy, we derive a higher order approximation.

## ARTICLE INFO

### Article history:

Received 29 April 2014

Received in revised form

11 August 2014

Accepted 13 August 2014

Available online 21 August 2014

### Keywords:

Integrodifference equations

Species invasion

Heterogeneity

Conservation

Dispersal

## ABSTRACT

Characterising the spread of biological populations is crucial in responding to both biological invasions and the shifting of habitat under climate change. Spreading speeds can be studied through mathematical models such as the discrete-time integro-difference equation (IDE) framework. The usual approach in implementing IDE models has been to ignore spatial variation in the demographic and dispersal parameters and to assume that these are spatially homogeneous. On the other hand, real landscapes are rarely spatially uniform with environmental variation being very important in determining biological spread. This raises the question of under what circumstances spatial structure need not be modelled explicitly. Recent work has shown that spatial variation can be ignored for the specific case where the scale of landscape variation is much smaller than the spreading population's dispersal scale. We consider more general types of landscape, where the spatial scales of environmental variation are arbitrarily large, but the maximum change in environmental parameters is relatively small. We find that the difference between the wave-speeds of populations spreading in a spatially structured periodic landscape and its homogenisation is, in general, proportional to  $\epsilon^2$ , where  $\epsilon$  governs the degree of environmental variation. For stochastically generated landscapes we numerically demonstrate that the error decays faster than  $\epsilon$ . In both cases, this means that for sufficiently small  $\epsilon$ , the homogeneous approximation is better than might be expected. Hence, in many situations, the precise details of the landscape can be ignored in favour of spatially homogeneous parameters. This means that field ecologists can use the homogeneous IDE as a relatively simple modelling tool – in terms of both measuring parameter values and doing the modelling itself. However, as  $\epsilon$  increases, this homogeneous approximation loses its accuracy. The change in wave-speed due to the extrinsic (landscape) variation can be positive or negative, which is in contrast to the reduction in wave-speed caused by intrinsic stochasticity. To deal with the loss of accuracy as  $\epsilon$  increases, we formulate a second-order approximation to the wave-speed for periodic landscapes and compare both approximations against the results of numerical simulation and show that they are both accurate for the range of landscapes considered.

© 2014 Elsevier Ltd. All rights reserved.

\* Corresponding author at: Wolfson Centre for Mathematical Biology, Mathematical Institute, Radcliffe Observatory Quarter, Woodstock Road, Oxford, Oxfordshire OX2 6GG, UK.

E-mail addresses: [gilbert@maths.ox.ac.uk](mailto:gilbert@maths.ox.ac.uk) (M.A. Gilbert), [gaffney@maths.ox.ac.uk](mailto:gaffney@maths.ox.ac.uk) (E.A. Gaffney), [jmbul@ceh.ac.uk](mailto:jmbul@ceh.ac.uk) (J.M. Bullock), [smwhit@ceh.ac.uk](mailto:smwhit@ceh.ac.uk) (S.M. White).

<http://dx.doi.org/10.1016/j.jtbi.2014.08.022>

0022-5193/© 2014 Elsevier Ltd. All rights reserved.

## 1. Introduction

Understanding the changing spatial distributions of plant populations is of utmost importance to ecologists, environmental managers, conservationists (Hulme, 2006) and agronomists (Pimentel et al., 2005). This is due to both the sizeable environmental and

economic impacts of biological invasions (Pimentel et al., 2005; Williamson, 1999; Pyšek and Richardson, 2010; Vitousek et al., 1993) and the need for species to keep pace with shifting habitat if they are to survive the effects of climate change (Zhou and Kot, 2011; Bennie et al., 2013; Bullock et al., 2012). Developing the understanding of spatial spread through mathematical modelling should enhance our ability to manage invasive species and the ecological effects of climate change (e.g. Travis et al., 2013).

Both extrinsic (landscape) and intrinsic (individual) variation have been found to be important factors in determining whether a population spreads and its spread rate. Lewis (2000) found that the effect of intrinsic variation is to reduce a population's ability to spread and its spreading speed. In contrast, while landscape structure is a decisive factor in determining whether a population spreads and its spreading speed (Bennie et al., 2013; King and With, 2002), its precise influence on spread is more complicated. Mathematical models of population spread have addressed landscape structure in two ways (e.g. Shigesada et al., 1986; Dewhurst and Lutscher, 2009). At one extreme, models have been developed to explicitly represent fragmented landscapes (Gilbert et al., 2014) while at the other extreme, many researchers have treated landscapes as homogeneous (Skellam, 1951; Levin, 1974; Kot et al., 1996; Neubert and Caswell, 2000). One might expect that neglecting to incorporate the landscape structure explicitly would result in inaccurate predictions of spread. However, homogeneous approximations have been relatively successful when compared with real data, for example Bullock et al. (2008) and Caswell et al. (2003). Here, we will address the question of under what circumstances the details of landscape structure can be ignored, and when they must be taken into account if accurate predictions are to be made.

We use an Integrodifference Equation (IDE) framework (Kot and Schaffer, 1986) to model spreading populations. IDEs treat reproduction/maturation and dispersal as separate sequential phases in an (e.g. annual) cycle and have been widely used to study population spread, especially in plants (Bullock et al., 2008, 2012; Neubert and Parker, 2004; Schreiber and Ryan, 2011; Skarpaas and Shea, 2007). IDEs can incorporate stage-structured matrix population models (Neubert and Caswell, 2000) and any dispersal pattern that can be formulated as a *dispersal kernel*, the distribution of displacements of individuals from their original position, or (for juveniles) the position of their parent. Landscape heterogeneity can be introduced to the model in terms of spatially heterogeneous parameters in the dispersal kernel or the population projection matrix. We refer the reader to the following key papers which develop the theory of non-stage-structured IDEs: Kot and Schaffer (1986), Kot et al. (1996), and Weinberger (1982); stage-structured IDEs: Neubert and Caswell (2000), Neubert and Parker (2004), and Garnier and Lecomte (2006); spatially heterogeneous IDEs: Dewhurst and Lutscher (2009), Weinberger (2002), and Weinberger et al. (2008). For a full derivation of the stage structured model, see Neubert and Caswell (2000). In the interest of brevity, we give only a brief overview of this derivation.

In particular, the general stage-structured, spatially heterogeneous IDE (Neubert and Caswell, 2000) in one spatial dimension relates the continuous population distribution at time  $t+1$  with the vector valued stage-structured distribution  $\mathbf{u}^t(x)$  at time  $t$  and location  $x \in \mathbb{R}$ , via

$$\mathbf{u}^{t+1}(x) = \int_{-\infty}^{\infty} [\mathbf{K}(x-y, y) \circ \mathbf{B}(\mathbf{u}^t(y), y)] \mathbf{u}^t(y) dy, \quad (1)$$

where  $\circ$  denotes the Hadamard (elementwise) product of two matrices (Neubert and Caswell, 2000). This relation is non-dimensional in that we do not give scales or units to length, population density or time, with the analysis applicable to all choices of length and time scales. In the integrand  $\mathbf{B}(\mathbf{u}^t(y), y)$  is the

population projection matrix, with its  $(i,j)$ th entry being the ratio of the number of individuals in stage  $j$  after the growth phase and the number of individuals in stage  $i$  at time  $t$  (at location  $y$ ).  $\mathbf{K}(x-y, y)$  is the matrix of dispersal kernels  $K_{ij}(x-y, y)$  for individuals which transitioned from stage  $j$  to stage  $i$  in the growth phase. It is necessary to consider the dispersal pattern of individuals transitioning between each (permitted) pair of demographic stages separately, as the stage of the individual or, in the case of juveniles, its parent before the growth phase will often affect the individual's dispersal behaviour. For example, for plants with wind dispersed seeds, the mean dispersal distance of a seed/new juvenile will depend on the seed release height of its parent and therefore on its parent's demographic stage (e.g. Travis et al., 2011).

The long-term behaviour and spreading speeds of solutions to (1) can be studied through numerical simulation. However, analytical expressions for the persistence and spreading speed are very useful in understanding parameter dependencies. Additionally, their calculation is much less computationally expensive than numerical simulation, so allow extensive parameter sweeps when calculating the effects of different factors on the speed at which the population propagates, the *wave-speed*.

For spatially homogeneous IDEs with no Allee effect we can find a simple expression for the wave-speed as long as this wave-speed is *linearly determined* and constant, rather than accelerating, or asymptotically infinite. This is guaranteed under the assumptions given by Li et al. (2005). Under these assumptions, the asymptotic wave-speed is given by

$$\hat{c} = \min_{s > 0} \left( \frac{1}{s} \log(\rho(s)) \right) \quad (2)$$

where  $\rho(s)$  is the principal (largest in absolute value) eigenvalue of the operator

$$\mathbf{H}(s) = \int_{-\infty}^{\infty} [\mathbf{K}(z) \circ \mathbf{A}] e^{sz} dz. \quad (3)$$

For spatially heterogeneous IDEs, no equivalent expression exists. This has led to the development of several analytical approximations for the wave-speed in different scenarios and asymptotic limits. Due to their relative tractability, these analyses have focused on *periodic landscapes* of alternate ('good' and 'bad') patches with different values for the growth and dispersal parameters. Mathematically, this means that the operator on the RHS of (1) is a *periodic operator* (Weinberger, 2002), i.e. it is invariant under translations of distance  $nL$ , where  $L$  is the period of the landscape and  $n \in \mathbb{Z}$ . Kawasaki and Shigesada (2007) developed approximations for cases when dispersal is given by the Laplace (exponential) kernel (Kawasaki and Shigesada, 2007). Other researchers have developed approximations applicable to any exponentially bounded kernel, but where certain parameters in the model must be related to each other by a small parameter  $\epsilon \ll 1$  (with smaller  $\epsilon$  giving a greater degree of accuracy). Dewhurst and Lutscher (2009) considered landscapes where the period of the landscape is much smaller than the scale of dispersal. They used *averaging techniques*, replacing the spatially heterogeneous parameters with their spatial homogenisation (average), allowing the use of results for homogeneous landscapes. Gilbert et al. (2014) found approximations for periodic landscapes in which the spatial scale of the good patches is much smaller than the scale of dispersal and the demographic rates in the good patches are much greater than those in the bad patches.

The existing approximations give accurate results (when compared with numerical simulation) for spreading speeds of populations with a particular dispersal kernel or in the relevant asymptotic limit. In contrast to previous studies, in this paper we will derive results for landscapes with low environmental variation, in which the environmentally driven variation  $\epsilon$  in

Download English Version:

<https://daneshyari.com/en/article/6370264>

Download Persian Version:

<https://daneshyari.com/article/6370264>

[Daneshyari.com](https://daneshyari.com)