Spreading speeds for stage structured plant populations in fragmented landscapes

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HIGHLIGHTS

- We consider integrodifference equations in periodic heterogeneous landscapes.
- We derive novel analytical approximations to the wave-speed.
- Crucially, the landscape period is not constrained by the dispersal scale.
- We demonstrate high accuracy of the approximation through numerical simulation.
- We find that the choice of dispersal kernel has a large effect on the wave-speed.

ARTICLE INFO

ABSTRACT

Landscape fragmentation has huge ecological and economic implications and affects the spatial dynamics of many plant species. Determining the speed of population spread in fragmented/hetero-geneous landscapes is therefore of utmost importance to ecologists. Stage-structured integrodifference equations (IDEs) are deterministic models which accurately reflect the life cycles and dispersal patterns for numerous species. Existing approximations to wave-speeds consider only particular kernels, or landscapes in which the scale of variation is much smaller than the dispersal scale. We propose an analytical approximation to the wave-speeds of IDE solutions with periodic landscapes of alternating good and bad patches, where the dispersal scale is greater than the extent of each good patch and where the ratio of the demographic rates in the good and bad patches is given by a small parameter, denoted as ε. We formulate this approximation for the Gaussian and Laplace dispersal kernels and for stage structured and non-stage structured populations, and compare the results against numerical simulations. We find that the approximation is accurate for the landscapes considered, and that the type of dispersal kernel affects the relationship between landscape structure, as classified by landscape period and good patch size, and the spreading speed. This indicates that accurately fitting a kernel to data is important in determining the relationship between landscape structure and spreading speed.

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1. Introduction

The spread of plant populations has significant ecological and economic implications. Invasions by introduced plant species cause ecosystem degradation, loss of biodiversity (Williamson, 1999), have detrimental impacts on human health and well-being (Pyšek and Richardson, 2010), increase the rate of extinctions (Vitousek et al., 1996) and cost nations hundreds of billions of US

dollars per year (Pimentel et al., 2005). Conversely, in a conservation context, as the climate changes and the location of suitable habitat shifts, a native species' ability to survive will depend on its ability to spread at an equal or greater rate than that at which its habitat shifts (Zhou and Kot, 2011; Bennie et al., 2013; Bullock et al., 2012). Therefore, understanding the process by which a species' range expands is of utmost importance, and an area of ongoing interest in ecology.

Most mathematical models of species' range expansion consider only spatially homogeneous landscapes (e.g. Bullock et al., 2012) in which the demographic and dispersal parameters do not vary in space. However, landscape structure is very important in determining a species' ability to spread and its spreading speed (Bennie et al., 2013; King and With, 2002). Landscape structure affects both dispersal and demographic processes, and is therefore

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of particular importance given the extent to which *fragmentation* affects the area and spatial distribution of habitats (Hooftman and Bullock, 2012). Fragmentation consists of two processes, the loss of suitable habitat and the increasing isolation of remaining habitat patches. It is a global phenomenon (Fischer and Lindenmayer, 2007), which increases the vulnerability of landscapes to species invasion (Marvier et al., 2004; Knops et al., 1995) and may reduce species' ability to track regions of suitable climate as these regions shift (Hodgson et al., 2012; Renton et al., 2012).

Plant populations are often studied using stage-structured matrix models (Caswell, 2000), which can incorporate the different characteristics of a species at different points in its life-cycle. Such stage-structured representation can be incorporated into integrodifference equations (Kot and Schaffer, 1986), which are often used to model population spread in plants (Bullock et al., 2008, 2012; Neubert and Parker, 2004; Schreiber and Ryan, 2011; Skarpaas and Shea, 2007). Continuous time, *age-structured* models have also been used (Van den Bosch et al., 1992). We choose IDEs as our model as they incorporate important aspects of plant population behaviour: (1) they treat time as a discrete quantity, so accurately reflect the seasonal growth and dispersal of many plant species, and (2) incorporate different dispersal kernels to model various dispersal mechanisms. Spatial structure is generally continuous, although spatially discrete IDEs (or Coupled Map Lattices) have been studied (White and White, 2005).

A simple non-stage-structured IDE relates the continuous population distribution $u^{t+1}(x)$ at time $t+1$, with the scalar distribution $u^t(x)$ at integer time t, where $x \in \mathbb{R}$ is a location in one dimensional space, via

$$u^{t+1}(x) = \int_{-\infty}^{\infty} k(x-y, y) f(u^t(y), y) u^t(y) \, dy. \tag{1}$$

In the growth phase, the population distribution is multiplied by the density and location dependent *growth rate* $f(u^t(y), y)$ (Neubert and Caswell, 2000; Caswell et al., 2003; Coutinho et al., 2012; Zhou and Kot, 2011). For the dispersal phase, the value of the post-dispersal population distribution at x is obtained by taking the spatial integral of the product of the pre-dispersal population, $f(u^t(y), y) u^t(y)$ and the *dispersal kernel* $k(x-y, y)$, the relative density of dispersal from y to x (Kot et al., 1996). In other words, the population abundance at spatial location x at the next generation is simply the contribution from the birth/death processes, f, of the current generation that move to location x according to redistribution kernel, k. Hence, the spatio-temporal population dynamics heavily depend on the growth and dispersal functions.

The long-term behaviour of solutions to IDEs can be studied through simulation, but analytical results are very useful, in that they help understand qualitative behaviour and dependencies on particular parameters, and provide a less computationally expensive way to study the dynamics of solutions to IDEs. For homogeneous IDEs with no Allee effect, where the growth and dispersal parameters are independent of location and the intrinsic growth rate $f(0, y)$ is higher than the growth rate experienced by any non-zero population $f(u, y)$, straightforward analytical expressions for the wave-speed have been derived (Kot et al., 1996). For spatially heterogeneous IDEs, where the growth and dispersal parameters vary spatially, the analysis is less straightforward.

The solution of a spatially homogeneous IDE with no Allee effect is an exponential travelling wave (Kot, 1992), with the spreading behaviour being governed by the behaviour of the solution's wave-front (van den Bosch et al., 1990). This is often referred to as the *Linear Conjecture* (Mollison, 1991), and allows us to approximate the IDE by its linearisation. For an homogeneous IDE, the growth rate $f(u^t(y), y)$ has no explicit y dependence, allowing us to write it as $f(u^t(y))$. The dispersal kernel $k(x-y, y)$ depends only on the distance $|x-y|$ travelled by the propagule, and has no explicit

dependence on the origin y of the propagule, allowing us to write it as $k(x-y)$. Given these conditions, Weinberger (1982) showed that the asymptotic wave-speed for travelling wave solutions of (1) with bounded initial support is given by

$$\hat{c} = \min_{s > 0} \left(\frac{1}{s} \log \left(f(0) M(s) \right) \right) \tag{2}$$

where $M(s)$ is the moment generating function (MGF) of the dispersal kernel $k(x-y)$, $M(s) = \int_{-\infty}^{\infty} k(z) e^{sz} \, dz$. Neubert and Caswell (2000) incorporated stage structure into homogeneous IDEs, with the asymptotic wave-speed being given by

$$\hat{c} = \min_{s > 0} \left(\frac{1}{s} \log \left(\rho(s) \right) \right) \tag{3}$$

where $\rho(s)$ is the principal eigenvalue of the operator

$$\mathbf{H}(s) = \int_{-\infty}^{\infty} [\mathbf{K}(z) \circ \mathbf{A}] e^{sz} \, dz, \tag{4}$$

where $\circ$ denotes the Hadamard (elementwise) product of two matrices, $\mathbf{K}(z)$ denotes the stage structured dispersal kernel and $\mathbf{A}$ the stage-structured population projection matrix linearised around the zero population state (Neubert and Caswell, 2000).

For spatially heterogeneous IDEs, the lack of an equivalent expression to (2) has necessitated the development of other approaches to determine population persistence (Van Kirk and Lewis, 1997; Lutscher and Lewis, 2004), invasion conditions and wave-speeds (Dewhirst and Lutscher, 2009). All the existing approaches consider *periodic landscapes*, where the landscape is partitioned into periodically alternating *good* and *bad* patches, with the demographic rates and dispersal parameters taking fixed values in the different patch types. Kawasaki and Shigesada (2007) analysed the special case of the Laplace (exponential) dispersal kernel and used the piecewise separability of the spatial variables in the kernel to derive conditions and speeds for invasions in periodic landscapes. Dewhirst and Lutscher (2009) used *averaging* techniques to derive conditions and speeds for any exponentially bounded dispersal kernel in landscapes where the period of the landscape is much smaller than the scale of dispersal (although numerically the approximation has been found to work outside this range, up to the point where the dispersal scale and landscape period are of the same order). This difference in scales allows the replacement of the $f(0)M(s)$ term in (2) with the average of the two corresponding expressions for the good and bad patches to get the asymptotic wave speed of a non-stage structured IDE on a periodic landscape. The existing analytical methods have been successful in their agreement with simulations of IDEs, but are limited to non-stage-structured populations and either (i) to a particular choice of kernel, which does not accurately describe the dispersal patterns of all species, e.g. Samia and Lutscher (2010), or (ii) to cases in which dispersal occurs at scales much larger than the distance between patches (Fig. 1a), see Dewhirst and Lutscher (2009) and Samia and Lutscher, 2010. However, many fragmented habitats (Fahrig, 2003) such as calcareous grassland in Dorset, UK (Hooftman and Bullock, 2012) and woodland in Wisconsin (Curtis, 1956), as well as natural habitats such as vernal pools in California (Holland and Jain, 1981), do not conform to this pattern and are composed of small habitat fragments separated by distances which have sufficient length to make inter-patch dispersal rare. Hence, for general dispersal kernels, the spread of species in such landscapes cannot be analysed by existing methods. There is therefore a need for analytical approximations of invasion speeds which can incorporate a wide range of dispersal scales and kernels, stage structure and landscape heterogeneity, and are appropriate to a broader class of landscapes.

In this paper, we will address this important gap, and will derive analytical approximations for the asymptotic invasion speeds of stage structured populations in landscapes where (i) the spatial extent of good habitat patches is smaller than the scale of dispersal