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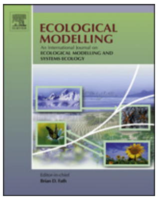

Invasion with stage-structured coupled map lattices: Application to the spread of scentless chamomile

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ABSTRACT

Two fundamental aspects of invasion dynamics are population growth and population spread. These quantities have been subject of study in biological invasions and can be used to study management and control of organisms. In this paper we derive formulae to calculate wave speed and rates of spread for coupled map lattices. Coupled map lattice models are dynamical models where space and time are discrete. We also show how wave speed and rate of spread can be calculated for structured population coupled map lattices in deterministic, stochastic environments and heterogeneous landscapes. Coupled map lattices are simple mathematical models that can be easily linked to landscape data to study invading organisms control strategies.

1. Introduction

Two fundamental aspects of invasion dynamics are population growth and population spread. The two related quantities (intrinsic growth rate and rate of spread) are essential to invasion theory. They have been the subject of study in mathematical models for invasions (Hastings et al., 2005), and the quantities are key control parameters in conservation management and biological control (Fagan et al., 2002; Shea, 2004; Neubert and Parker, 2004; Allen et al., 1996). Because of the long time and broad spatial scales at which invasions occur, the use of models is essential to understand the dynamics of invasions and design possible management and conservation strategies.

There are several modelling strategies for population growth and spatial spread: partial differential equations, integro-difference equations, coupled map lattices, and cellular automata. Partial differential equations incorporate continuous space and time, integro-difference equations, discrete time and continuous space, and coupled map lattice, discrete time and space. For cellular automata, in addition to time and space being discrete, the state space is also discrete. Which modelling strategy is the best depends upon the dynamical characteristics of the system under analysis, and upon spatio-temporal scales. In the last two decades there has been an increase in the use of discrete models due to their ability to incorporate stochastic components and local inhomogeneities (Durrett and Levin, 1994), and because personal computers now allow for fast numerical computations.

Integro-difference equation (IDE) models are discrete-time and continuous-space models, that incorporate dispersal data directly using a kernel function (Kot et al., 1996). This dispersal kernel allows for the redistribution of individuals in continuous space. These models have been widely used to study spatial dynamics and control of invasive species (e.g. Allen et al., 1996; Buckley et al., 2005; Kot et al., 1996). Mathematically an IDE is defined as

$$n_{t+1}(x) = \int_{-\infty}^{\infty} \underbrace{k(x,y)}_{\text{dispersal from } y \text{ to } x} \underbrace{f[n_t(y)]}_{\text{growth at } y}\, dy. \qquad (1)$$

Here $n_t(x)$ is population density at time t location x and $f[n_t(y)]$ describes population growth. The dispersal kernel $k(x,y)$ is a probability density function describing the likelihood of dispersal to point x.

Coupled map lattices (CMLs) are models where space and time are discrete, and whose structure is similar to IDEs. Some CMLs have been used to study host–parasitoid interactions (Hassell et al., 1991; Kean and Barlow, 2001; Bjornstad and Bascompte, 2001; Bonsall and Hassell, 2000), metapopulation level applications (Janosi and Scheuring, 1997), applied biological control (Rees and Paynter, 1997; Rees and Hill, 2001), and tree dispersal (Jiang and Zhang, 2008). A coupled map lattice is a dynamical system where

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time and space are discrete, and the state variable is continuous (White and White, 2005; Kaneko, 1992).

As with integro-difference equations, a CML describes the growth and dispersal of the population, but now on a discrete lattice. Strictly, a CML only involves local interactions, meaning dispersal occurs in a local neighbourhood Ω. However, there is no restriction on how large Ω is. Consider the continuous spatial domain $\bar{X}$. A one-dimensional discrete regular lattice over $\bar{X}$ is defined as $X = \{x_{-\infty}, \ldots, x_0, \ldots, x_{-\infty}\}$, with $x_i = ih$, where h is the cell size (scale) of the lattice and i is an integer. Mathematically a CML can be defined,

$$n_{t+1}(x_i) = \sum_{x_j \in \Omega} \underbrace{k(x_i, x_j)}_{\text{dispersal from } x_j \text{ to } x_i} \underbrace{f[n_t(x_j)]}_{\text{growth at } x_j}, \tag{2}$$

where x_i, x_j are points in a one-dimensional lattice, $n_t(x_i)$ is population at time t location x_i, $f[n_t(x_i)]$ is a map that models population growth and $k(x_i, x_j)$ is a discrete probability mass function for dispersal. In a spatially homogeneous environment, dispersal kernels that only depend on signed distance $x_d = x_i - x_j$ are called difference kernels. As an example of a difference kernel $k(x_d)$, $x_d = x_i - x_j$, consider,

$$k(x_d) = \begin{cases} (1-u) & \text{if } x_d = 0 \\ \dfrac{u}{|\Omega| - 1}, & \text{otherwise} \end{cases} \tag{3}$$

where $|\Omega|$ is the number of cells in the neighbourhood Ω. Note that $u \in [0, 1]$ and $\sum_{\Omega} k(x_d) = 1$. When $|\Omega| = 3$, this example is considered a classic CML model with nearest neighbour interaction. CMLs can be extended to a two-dimensional spatial lattice. Here the nearest neighbour interactions, in a Moore neighbourhood, involve the central lattice point and eight neighbours so that $|\Omega| = 9$.

Some comparative studies show how results can be obtained using CMLs are similar to those found with other modelling structures like IDEs and individual-based models (White and White, 2005; Brannstrom and Sumpter, 2005). As we will show here, analytical tools developed for IDEs can be used directly to study spread in discrete space for structured population models.

In this paper we apply tools developed for calculation of wave speed and spread rate in integro-difference equations to coupled map lattices. To our knowledge, the application of these to CMLs is new. We use CMLs to study the population dynamics and spread of structured populations with applications to a particular invader, scentless chamomile (*Matricaria perforata*), an introduced annual, biennial or short-lived perennial plant that has become a widely distributed weed in cultivated areas in North America (Hinz, 1996; Hinz and McClay, 2000). We further analyze possible control strategies, and explore CMLs in heterogeneous landscapes and stochastic environments.

2. Discrete structured spatial models

2.1. Matrix coupled map lattice equations

Matrix population models have been shown to be an effective tool to study population growth and control (Shea and Kelly, 1998; van den Driessche and Watmough, 2002; Parker, 2000; McLeod and Saunders, 2001). Space can be incorporated in the matrix model formulation by extending a structured population across space, and considering dispersal between these locations in a continuous or discrete domain. Here we consider stage-structured models with discrete space which we will call Matrix CML. For continuous space stage-structured models see Neubert and Caswell (2000). A matrix CML equation with stage structure is described by

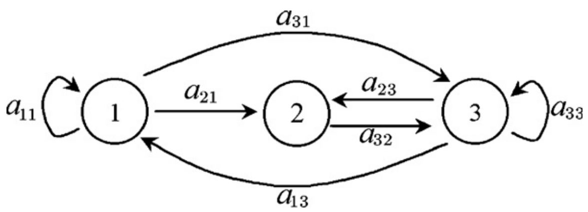

Fig. 1. Life cycle graph of scentless chamomile. Node 1: seed bank, node 2: rosettes, and node 3: flowering plants.

$$\mathbf{n}_{t+1}(x_i) = \sum_{x_j \in \Omega} [\tilde{\mathbf{K}}(x_i, x_j) \circ \mathbf{A}]\mathbf{n}_t(x_j). \tag{4}$$

Here $\mathbf{A}$ is the projection matrix, $\mathbf{n}_t(x_i)$ is a vector of stages at time t location x_i and $\tilde{\mathbf{K}}$ is a matrix of discrete kernels whose elements $\tilde{k}_{lm}(x, y)$ are kernels that describe dispersal as the individual moves from location y to x from stage m to stage l. Each entry of $\tilde{\mathbf{K}}(x_i, x_j) = [\tilde{k}_{lm}(x_i, x_j)]$ must satisfy:

$$\sum_{i=-\infty}^{\infty} \tilde{k}_{lm}(x_i, x_j) = 1, \tag{5}$$

If difference kernels are assumed then $\tilde{\mathbf{K}}(x_i - x_j)$. The symbol "$\circ$" denotes Hadamard product which is element-wise multiplication. It is assumed that the $m \times m$ matrix $\mathbf{A}$ is non-negative and primitive; hence there is a real and positive dominant eigenvalue λ that corresponds to the population growth rate. For detailed definition and examples of matrix models (see Caswell, 2001).

As an example, consider the matrix model for scentless chamomile (SC) from de Camino-Beck and Lewis (2007). Fig. 1 describes the scentless chamomile life cycle graph. The projection interval for this model is 1 year. Nodes 1, 2 and 3 correspond to seeds, rosettes and flowering plant stages. In the life cycle, seeds can germinate and produce either rosettes (stage without flowers) or flowering plants, or stay in the seed bank. Rosettes can survive over winter producing a flowering plant next year. The projection matrix of scentless chamomile is given by

$$\mathbf{A} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}. \tag{6}$$

Since only seeds disperse (the third column of the matrix), the dispersal matrix is given by difference kernels

$$\tilde{\mathbf{K}}(x_i, x_j) = \tilde{\mathbf{K}}(x_i - x_j) = \begin{bmatrix} \Delta(x_i - x_j) & \Delta(x_i - x_j) & \tilde{k}(x_i - x_j) \\ \Delta(x_i - x_j) & \Delta(x_i - x_j) & \tilde{k}(x_i - x_j) \\ \Delta(x_i - x_j) & \Delta(x_i - x_j) & \tilde{k}(x_i - x_j) \end{bmatrix}, \tag{7}$$

Here $\tilde{k}(z)$, $z = x - y$ is the dispersal kernel describing the dispersal of seeds and the discrete delta function $\Delta(x_i - x_j)$, defined as

$$\Delta(x_i - x_j) = \delta_{ij} = \begin{cases} 1, & \text{if } i = j \\ 0, & \text{otherwise} \end{cases}, \tag{8}$$

is used for transitions where no dispersal occurs. As can be seen from the third column of matrix $\tilde{\mathbf{K}}(z)$, seeds, produced by flowering plants, disperse and can remain as seeds, germinate to rosettes, or germinate to flowers in a single year.

A dispersal kernel can be defined using mechanistic principles, or can be obtained directly from data without assuming any particular shape (Lewis et al., 2005). Consider the example when relative frequencies of disperser f_j, are collected in two directions and at