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Bounds for the critical speed of climate-driven moving-habitat models

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ABSTRACT

Integrodifference equations have recently been used as models for populations undergoing climate-driven habitat movement. In these models, the persistence of a population is governed by the maximal or dominant eigenvalue of a Fredholm integral equation with an asymmetric kernel; this eigenvalue determines the critical translational speed for extinction of the population. Since direct methods for finding eigenvalues are often analytically or computationally expensive, we explored the extensive literature on alternative methods for localizing maximal eigenvalues. We found that a sequence of iterated row sums provide upper and lower bounds for the maximal eigenvalue. Alternatively, arithmetic and geometric symmetrization yield upper and lower bounds. Geometric symmetrization is especially valuable and leads to a simple Rayleigh quotient that can be used to analytically approximate the critical-speed curve. Our research sheds new light on the interpretation and limitations of the average-dispersal-success approximation; it also provides a generalization of this useful tool for asymmetric kernels.

1. Introduction

The Earth is getting warmer. Many species have responded to this warming by shifting their distributions [1–3]. High velocities of climate change [4,5] can, however, reduce population sizes and threaten species [6,7].

Recently, Zhou and Kot [8,9] used the integrodifference equation (IDE)

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y) f[n_t(y)]\, dy \tag{1}$$

to study climate-driven populations. This model maps the density of a population in generation t, $n_t(x)$, to a new density, $n_{t+1}(x)$, in two discrete stages. During the first (or sedentary) stage, individuals inside a habitat patch, the interval $[-L/2+ct,\ L/2+ct]$, grow, reproduce, and die. At each point x inside the interval, the local population, $n_t(x)$, produces $f[n_t(x)]$ propagules. The interval, initially $[-L/2,\ L/2]$, moves to the right, because of climate change, with translational speed c. During the second (or dispersal) stage, propagules disseminate. The dispersal kernel $k(x)$ is the (nonnegative) probability density function for the displacement of propagules. A convolution integral tallies the contributions from all sources y, in the interval $[-L/2+ct,\ L/2+ct]$, to each destination x (both inside and outside the habitat patch).

Analyses of model (1) suggest that a moving habitat can have a profound effect on the dynamics of a population. Speed, in general, kills. Rapid translational shifts lead to ineffective dispersal (as propagules fall behind a moving habitat patch) and to either death or reproductive failure. For each growth rate, patch size, and dispersal kernel, there exists a critical translational speed beyond which the population goes extinct. Zhou and Kot [8,9] developed methods for determining this critical speed. Harsch et al. [10] extended model (1) to age- and stage-structured populations. Potapov and Lewis [11], Berestycki et al. [12], and Leroux et al. [13], in turn, obtained similar results using reaction–diffusion models.

One advantage of model (1) is that it quickly engenders a simple eigenvalue problem that determines the viability of a moving population. The critical speed is typically found by looking for translational speeds that cause the maximal eigenvalue, the positive real eigenvalue of largest modulus, to equal one.

The most direct methods for finding the maximal eigenvalue are to find and order all the eigenvalues or to use simple numerical methods, such as the power method, that generate dominant eigenvalues. These methods are often analytically or computationally expensive. There is also, however, a large literature, going back to Frobenius [14], dedicated to localizing maximal eigenvalues by other means. We performed an exhaustive survey of this literature and report on several efficient methods for determining tight upper and lower bounds on the critical speed of extinction.

In Section 2, we quickly derive the eigenvalue problem for the viability of a moving population and review the methods that have been used to determine the critical speed of extinction. We also

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discuss the strengths and weaknesses of these methods. In Section 3, we review classical methods for localizing maximal eigenvalues and show how iterated row (and column) sums [15,16] can be used to bound the critical speed of extinction. In Section 4, we use recent results on the symmetrization of matrices [17–19] to obtain upper and lower bounds for critical-speed curves. In Section 5, we use geometric symmetrization to analytically approximate the critical-speed curves for two well-known kernels. Our results shed new light on the interpretation and limitations of the widely used average-dispersal-success approximation [20–23]. They also lead to an extension of this approximation for asymmetric kernels. We discuss these topics in Section 6.

2. Persistence

In the absence of Allee [24] effects, the persistence of a population governed by Eq. (1) is equivalent to instability of the trivial solution $n_t(x) = 0$. The stability of this trivial solution is, in turn, determined by the linear equation

$$n_{t+1}(x) = R_0 \int_{-L/2+ct}^{L/2+ct} k(x-y)\, n_t(y)\, dy, \tag{2}$$

where $R_0 = f'(0)$ is the net reproductive rate. Since we are interested in solutions that persist in a moving frame, we focus on perturbations to the trivial solution that can be written

$$n_t(x) = \lambda^t u(\bar{x}) \equiv \lambda^t u(x - ct). \tag{3}$$

This ansatz quickly generates the eigenvalue problem

$$\lambda\, u(x) = R_0 \int_{-L/2}^{L/2} k(x+c-y)\, u(y)\, dy, \tag{4}$$

where we have dropped the bars on $\bar{x}$ and $\bar{y}$ for notational convenience. (For the units to make sense, please note that c here is actually $c\Delta t$ with Δt equal to one.) See Zhou and Kot [8] for details.

Eq. (4) is a homogeneous Fredholm integral equation of the second kind. The kernel $k(x+c-y)$ of this integral equation is either nonnegative or positive. Because of the translational speed c, the kernel is not, in general, symmetric. The parameter λ is an eigenvalue; $u(x) \neq 0$ is the corresponding eigenfunction.

Eigenvalue problem (4) is nasty. If, however, our integral operator is compact (completely continuous), the problem simplifies. The eigenvalues then form a discrete set. This set may be finite, countably infinite, or empty [25]. Each eigenvalue has finite multiplicity and eigenvalues can only accumulate at zero. Compact integral operators act much like matrices.

To guarantee compactness, we will assume that $x \in [-L/2, L/2]$ and $y \in [-L/2, L/2]$ for finite L and that our kernel is a continuous function [26]. Thus, we assume that the environment is completely hostile outside the patch. See Hutson and Pym [27] for less restrictive conditions for compactness.

If the kernel is positive, we can also exploit [51] theorem. This theorem is analogous to the Perron–Frobenius theorem for positive matrices. If the conditions of this theorem are satisfied, eigenvalue problem (4) has a simple, positive eigenvalue of largest modulus (with a positive eigenfunction) that dominates all other eigenvalues. For sufficiently large R_0, the trivial solution then loses stability through $\lambda = 1$ as the translational speed decreases through the critical speed, and we can easily solve for the critical speed as a function of the other parameters in our model.

The restriction that the kernel is strictly positive is important [25]. If the kernel is only nonnegative, eigenvalues need not exist. If the kernel is only nonnegative and eigenvalues do exist, there is then a positive and real maximal eigenvalue at least as large as all other eigenvalues. This root may not, however, be simple, and there may be other eigenvalues of equal magnitude. This maximal eigenvalue has a nonnegative eigenfunction. We will assume, for convenience, that our kernel is strictly positive throughout this paper.

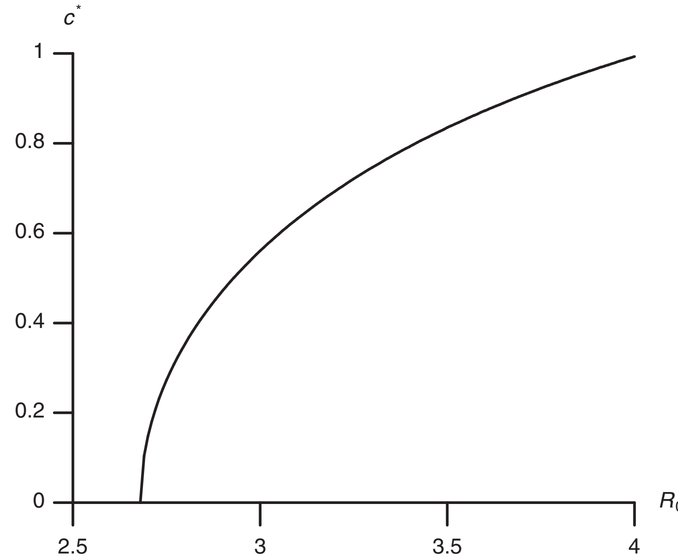

Fig. 1. A plot of the critical speed (for extinction) as a function of the net reproductive rate R_0 based upon Eq. (6) with patch size $L = 1$ and dispersal parameter $\omega = \pi/4$.

To date, we have solved eigenvalue problem (4) in three ways:

(a) Analytically

Eigenvalue problem (4) simplifies to a finite-dimensional problem in linear algebra if its kernel is separable (or degenerate). A kernel is separable [28,29] if it can be written as a finite sum, with each term in the sum the product of a function of x alone and a function of y alone. If a separable kernel is simple enough, the dominant eigenvalue and the critical speed c^* can be determined analytically.

For example, we can use the cosine angle-addition formula to reduce

$$k(x-y) = \begin{cases} \frac{\omega}{2} \cos \omega(x-y), & |x-y| \le \frac{\pi}{2\omega}, \\ 0, & |x-y| > \frac{\pi}{2\omega}, \end{cases} \tag{5}$$

to a positive, separable kernel for the case where the radius of dispersal, $\pi/(2\omega)$, is larger than the patch size and the shift speed c is sufficiently small. Zhou and Kot [8] thus showed that

$$c^* = \frac{1}{\omega} \cos^{-1}\left[\frac{16 + R_0^2\,(\omega^2 L^2 - \sin^2 \omega L)}{8\, R_0\, \omega\, L}\right] \tag{6}$$

(see Fig. 1). Speeds above this curve lead to extinction. Higher net reproductive rates R_0 allow higher shift speeds.

(b) Numerically

Eigenvalue problem (4) can also be solved using numerical methods such as Nyström's method [30,31]. This method discretizes the integral on the right-hand side of Eq. (4) using a quadrature rule and reduces the eigenvalue problem from that of an integral operator to that of a matrix.

Consider, for example, m spatial grid points, x_i or y_i, $i = 1, \ldots, m$, that divide the interval $[-L/2, L/2]$ into $m-1$ subintervals of equal length $\Delta y = L/(m-1)$. If we now use the repeated trapezoidal rule, Eq. (4) reduces to the matrix system

$$\lambda\, \mathbf{u} = R_0\, \mathbf{K}\, \mathbf{u}, \tag{7}$$

where $\mathbf{u}$ is now an $m \times 1$ vector of densities and $\mathbf{K}$ is an $m \times m$ matrix with elements k_{ij}, $i, j = 1, \ldots, m$, that are given in terms of the original