



A STOCHASTIC ANALYSIS OF INVASION OF EXOTIC SPECIES

S. Udayabaskaran* and N. G. Renganathan

School of Basic Sciences

Vel Tech Rangarajan Dr. Sagunthala

R&D Institute of Science and Technology

Avadi, Chennai 600 062

Tamilnadu, India

Abstract

We consider a microscopic stochastic model of invasion of exotic species in a lake system in a random environment. We obtain the speed of the invasion when the spatial density of the invasion is controlled by changing the offspring generating mechanism of invaders at the infected lake.

1. Introduction

Biological invasions on native communities have been very extensively studied in the past by several researchers (see for example the monograph of Williamson [11]). Lewis [4] has formulated a set of equations describing the dynamics of spatial moments of the population and analysed the effect of intrinsic stochastic factors when individuals interact locally over small neighborhoods. He has exhibited that the spread of invasion can be slowed

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*Corresponding author

down even in a uniform environment. Lewis and Pacala [5] derive integro-difference equations to describe a stochastic invasion process and use these equations to analyse the wave of invasion. Neubert et al. [6] have modelled invasions in fluctuating environments with discrete-time, continuous space, integro-difference equations which incorporate wide range of dispersal mechanisms that are common in empirical data, and they have described the effect of temporal fluctuations in both the population growth rate and the dispersal kernel on the speed of invasion in single-species. Olson and Roy [7] have considered the economics of controlling a biological invasion whose natural growth and spread is subject to environmental disturbances, and examined conditions under which it is optimal to eradicate the invasive species and conditions under which eradication is not optimal. Snyder [10] has considered a single-species invasion model and studied the impact of demographic stochasticity on the speed of biological invasions. Kot et al. [3] have linked deterministic integro-difference equations to stochastic, individual-based simulations by means of branching random walks, and using standard methods determined speeds of biological invasion for both average densities and furthest-forward individuals. Potapov et al. [9] have investigated an optimal control of biological invasions in lake networks. Kawasaki and Shigesada [2] have used an integro-difference model with the intrinsic growth rate specified by a spatially periodic step-function and the redistribution kernel given by an exponentially damping function to describe and analyse the spread of invading species on a periodically fragmented environment. Potapov et al. [9] have considered a meta-population model for Invasive Alien Species (IAS) in a lake network coupled with an economic model of prevention and characterized prevention methods controlling both the outflow of invaders at infected lakes and the inflow of invaders at uninfected lakes. Potapov and Lewis [8] have considered a model of invasion prevention in a system of lakes that are connected via traffic of recreational boats, and they showed that in presence of an Allee effect, the general optimal control problem is reduced to a significantly simpler stationary optimization problem of optimal invasion stopping. Finnoff et al. [1] have considered the problem of management of an aquatic invader spreading in a

lake system and generated control decisions and compared for an optimally controlled system and for a static optimization across asymptotic steady states. In almost all the above papers, the choice of spatial density function for the propagules has been macroscopically modeled to mimic the experimental data. However, the formulation of the density should be made based upon the microscopic considerations. In this paper, we fill this gap by considering a microscopic stochastic model of Invasion of Exotic Species (IES) in a lake system to analyse the speed of the invasion when the spatial density of the invasion is controlled by changing the offspring generating mechanism of invaders at the infected lake.

The lay out of the paper is as follows: Section 2 presents the stochastic model of the microscopic evolution of the cumulative invasion size $X(t, x)$ at time t and at distance x from the origin. In Section 3, the integro-difference equation for the generating function of $X(t, x)$ is obtained. The speed of invasion is analysed in Section 4. A spectral analysis of the invasion process is provided in Section 5. Section 6 presents a discussion of the findings of the present work and a conclusion.

2. The Stochastic Model of Invasion

We consider one-dimensional spatial invasion. We assume that one individual has invaded at time $t = 0$ and at the origin $x = 0$. This individual lives for one unit of time and splits into a random number ξ of offsprings. We assume that the offsprings inherit their parent unless otherwise specified and behave identically and independently. Let the offsprings disperse with redistribution kernel $k(x)$. Let $X(t, x)$ be the number of individuals in the interval $(-\infty, x]$ at time t , where $t = 0, 1, 2, \dots$. Since we start with one individual at the origin, we get

$$X(0, x) = \begin{cases} 0, & x < 0, \\ 1, & x \geq 0. \end{cases}$$

Clearly, $X(t, x)$ represents the number of individuals of the generation t

which are located with in the distance x from the origin. We assume that all individuals of a random generation change their reproductive capacity which alternates between two offspring generating functions $h^{(1)}(s) = \sum_0^\infty p_j^{(1)} s^j$ and $h^{(2)}(s) = \sum_0^\infty p_j^{(2)} s^j$ at random generation times t_1, t_2, \dots , where $0 < t_1 < t_2 < \dots$ and the random variables $t_1, t_2 - t_1, t_3 - t_2, \dots$ are independent and identically distributed. We assume that $t_0 = 0$ and

$$P\{t_{j+1} - t_j = k\} = (1 - \rho)^{k-1} \rho, \quad j = 0, 1, 2, \dots; \quad k = 1, 2, \dots$$

We note that all individuals existing at time t reproduce according to the offspring generating function $h^{(1)}(s)$, when $t_{2n} \leq t < t_{2n+1}$, $n = 0, 1, 2, \dots$ and those existing at time t reproduce according to the offspring generating function $h^{(2)}(s)$, when $t_{2n+1} \leq t < t_{2n+2}$, $n = 0, 1, 2, \dots$. We say that an e_1 -event occurs at the random time point t_n , $n = 0, 1, 2, \dots$ and an e_2 -event occurs at the random time point t_{2n+1} , $n = 0, 1, 2, \dots$. The propagules disseminate according to the dispersal kernel $k(x, y)$. The function $k(x, y)$ has the following interpretation:

$$\begin{aligned} & k(x, y) dy dx \\ = & \begin{cases} \text{Probability of an individual dispersing from } (y, y + dy) \text{ to } (x, x + dx) \\ \text{in one unit of time.} \end{cases} \end{aligned}$$

3. The Integro-difference Equation

To analyse the invasion process, we consider the generating function of $X(t, x)$ defined by

$$G(s, x; t) = E[s^{X(t, x)}].$$

Then, we have the initial condition

$$G(s, x; 0) = E[s^{X(0, x)}] = \begin{cases} 1, & x < 0, \\ s, & x \geq 0. \end{cases}$$

Using the Heaviside function $H(x)$, we can write the initial condition as follows:

$$G(s, x; 0) = 1 - H(x) + sH(x).$$

Since the offspring generating function of an individual at time t_0 is $h^{(1)}(s)$, we get

$$\begin{aligned} G(s, x; 1) &= \sum_{j=0}^{\infty} p_j^{(1)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 0) dx \right\}^j \\ &= h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 0) dx \right). \end{aligned}$$

To be specific, we observe that the offspring generating function of an individual time at $t = 1$ is either $h_1(s)$ with probability $1 - \rho$ or $h^{(2)}(s)$ with probability ρ , we get

$$\begin{aligned} G(s, x; 2) &= (1 - \rho) \sum_{j=0}^{\infty} p_j^{(1)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 1) dx \right\}^j \\ &\quad + \rho \sum_{j=0}^{\infty} p_j^{(2)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 1) dx \right\}^j \\ &= (1 - \rho) h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 1) dx \right) \\ &\quad + \rho h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 1) dx \right). \end{aligned}$$

Next, we observe that the offspring generating function of an individual at $t = 2$ is either $h^{(1)}(s)$ with probability $(1 - \rho)^2 + \rho^2$ or $h^{(2)}(s)$ with probability $2(1 - \rho)\rho$, we get

$$\begin{aligned}
G(s, x; 3) &= [(1 - \rho)^2 + \rho^2] \sum_{j=0}^{\infty} p_j^{(1)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 2) dx \right\}^j \\
&\quad + 2(1 - \rho)\rho \sum_{j=0}^{\infty} p_j^{(2)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 2) dx \right\}^j \\
&= [(1 - \rho)^2 + \rho^2] h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 2) dx \right) \\
&\quad + 2(1 - \rho)\rho h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 2) dx \right).
\end{aligned}$$

It is instructive to derive a similar equation for $G(s, x; 4)$. For this, we observe that the offspring generating function of an individual at $t = 3$ is either $h^{(1)}(s)$ with probability $(1 - \rho)^3 + 3\rho^2(1 - \rho)$ or $h^{(2)}(s)$ with probability $3(1 - \rho)^2\rho + \rho^3$, we get

$$\begin{aligned}
G(s, x; 4) &= [(1 - \rho)^3 + 3\rho^2(1 - \rho)] \sum_{j=0}^{\infty} p_j^{(1)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 3) dx \right\}^j \\
&\quad + [3(1 - \rho)^2\rho + \rho^3] \sum_{j=0}^{\infty} p_j^{(2)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 3) dx \right\}^j \\
&= [(1 - \rho)^3 + 3\rho^2(1 - \rho)] h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 3) dx \right) \\
&\quad + [3(1 - \rho)^2\rho + \rho^3] h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 3) dx \right).
\end{aligned}$$

Similarly, we obtain

$$\begin{aligned}
&G(s, x; 5) \\
&= [(1 - \rho)^4 + 6\rho^2(1 - \rho)^2 + \rho^4] \sum_{j=0}^{\infty} p_j^{(1)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 4) dx \right\}^j
\end{aligned}$$

$$\begin{aligned}
& + [4(1-\rho)^3\rho + 4\rho^3(1-\rho)] \sum_{j=0}^{\infty} p_j^{(2)} \left\{ \int_{-\infty}^{\infty} k(x, y) G(s, y; 4) dx \right\}^j \\
& = [(1-\rho)^4 + 6\rho^2(1-\rho)^2 + \rho^4] h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 4) dx \right) \\
& \quad + [4(1-\rho)^3\rho + 4\rho^3(1-\rho)] h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; 4) dx \right).
\end{aligned}$$

From the above form, we identify the general result

$$\begin{aligned}
& G(s, x; t+1) \\
& = A(t) h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; t) dx \right) + B(t) h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; t) dx \right),
\end{aligned}$$

where

$$A(t) = \sum_{j=0}^{\left\lfloor \frac{t}{2} \right\rfloor} \binom{t}{2j} p^{2j} (1-\rho)^{t-2j}, \quad B(t) = \sum_{j=0}^{\left\lfloor \frac{t}{2} \right\rfloor} \binom{t}{2j+1} p^{2j+1} (1-\rho)^{t-2j-1}.$$

We note that

$$\begin{aligned}
A(t) + B(t) &= \binom{t}{0} (1-\rho)^t + \binom{t}{1} \rho (1-\rho)^{t-1} + \binom{t}{2} \rho^2 (1-\rho)^{t-2} \\
&\quad + \cdots + \binom{t}{t} \rho^t = [(1-\rho) + \rho]^t = 1; \\
A(t) - B(t) &= \binom{t}{0} (1-\rho)^t - \binom{t}{1} \rho (1-\rho)^{t-1} + \binom{t}{2} \rho^2 (1-\rho)^{t-2} \\
&\quad - \cdots + (-1)^t \binom{t}{t} \rho^t = [(1-\rho) - \rho]^t = (1-2\rho)^t.
\end{aligned}$$

Consequently, we obtain

$$A(t) = \frac{1 + (1-2\rho)^t}{2}, \quad B(t) = \frac{1 - (1-2\rho)^t}{2}.$$

Theorem.

$$G(s, x; t+1) = \left[\frac{1 + (1-2\rho)^t}{2} \right] h^{(1)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; t) dx \right) \\ + \left[\frac{1 - (1-2\rho)^t}{2} \right] h^{(2)} \left(\int_{-\infty}^{\infty} k(x, y) G(s, y; t) dx \right). \quad (3.1)$$

Proof. The proof is obtained by applying the results of renewal theory. For this, we consider the random time points t_0, t_1, t_2, \dots . We note that the offspring generating function of all individuals existing at time t is $h^{(1)}(s)$ when $t_0 \leq t \leq t_1$. The offspring generating function for all individuals existing at time point t_1 is $h^{(2)}(s)$ and the offspring generating function for all individuals existing at all time points in the interval $t_1 \leq t \leq t_2$ is $h^{(2)}(s)$. Proceeding in this way, the offspring generating function of all individuals existing at an arbitrary generation time point t is either $h^{(1)}(s)$ or $h^{(2)}(s)$ according as $t_{2n} \leq t < t_{2n+1}$ or $t_{2n-1} \leq t < t_{2n}$. To study the probability structure of the random time points $t_0, t_1, t_2, t_3, t_4, \dots$, we define the following conditional distributions:

$$p_{ij}(n) = P \left\{ \begin{array}{l} n + r\text{th generation follows } h_j(s) \\ \text{as the offspring generating function} \\ \text{given that } r\text{th generation follows} \\ h_i(s) \text{ as the offspring generating function} \end{array} \right\},$$

$$n = 0, 1, 2, \dots; \quad i, j = 1, 2.$$

It is clear that $p_{ii}(0) = 1$, $i = 1, 2$. Using the Heaviside function $H(m)$, we obtain the following equations:

$$p_{11}(n) = (1-\rho)^n H(n) + H(n-2) \sum_{j=1}^{n-1} (1-\rho)^{j-1} \rho p_{21}(n-j), \quad (3.2)$$

$$p_{12}(n) = (1 - \rho)^{n-1} \rho H(n-1) + H(n-2) \sum_{j=1}^{n-1} (1 - \rho)^{j-1} \rho p_{22}(n-j), \quad (3.3)$$

$$p_{21}(n) = (1 - \rho)^{n-1} \rho H(n-1) + H(n-2) \sum_{j=1}^{n-1} (1 - \rho)^{j-1} \rho p_{11}(n-j), \quad (3.4)$$

$$p_{22}(n) = (1 - \rho)^n H(n) + H(n-2) \sum_{j=1}^{n-1} (1 - \rho)^{j-1} \rho p_{12}(n-j). \quad (3.5)$$

The above equations can be solved by generating function technique. We use the notation

$$\psi_{ij}(s) = \sum_{n=0}^{\infty} p_{ij}(n) s^n, \quad i, j = 1, 2.$$

Multiplying (3.2) by s^n and summing from $n = 0$ to ∞ , we get

$$\begin{aligned} \psi_{11}(s) &= \sum_{n=0}^{\infty} p_{11}(n) s^n \\ &= \sum_{n=0}^{\infty} (1 - \rho)^n s^n + \sum_{n=2}^{\infty} \sum_{j=1}^{n-1} (1 - \rho)^{j-1} \rho p_{21}(n-j) s^n \\ &= \frac{1}{1 - (1 - \rho)s} + \rho \sum_{j=1}^{\infty} (1 - \rho)^{j-1} \sum_{n=j+1}^{\infty} p_{21}(n-j) s^n \\ &= \frac{1}{1 - (1 - \rho)s} + \rho \sum_{j=1}^{\infty} (1 - \rho)^{j-1} \sum_{m=1}^{\infty} p_{21}(m) s^{m+j} \\ &= \frac{1}{1 - (1 - \rho)s} + \frac{s \rho \psi_{21}(s)}{1 - s(1 - \rho)}. \end{aligned} \quad (3.6)$$

Multiplying (3.3) by s^n and summing from $n = 0$ to ∞ , we get

$$\begin{aligned}
\psi_{12}(s) &= \sum_{n=0}^{\infty} p_{12}(n)s^n = \sum_{n=1}^{\infty} p_{12}(n)s^n = \sum_{n=1}^{\infty} (1-\rho)^{n-1} \rho s^n \\
&\quad + \sum_{n=2}^{\infty} \sum_{j=1}^{n-1} (1-\rho)^{j-1} \rho p_{22}(n-j)s^n \\
&= \frac{\rho s}{1-(1-\rho)s} + \rho \sum_{j=1}^{\infty} \sum_{n=j+1}^{\infty} (1-\rho)^{j-1} p_{22}(n-j)s^n \\
&= \frac{\rho s}{1-s(1-\rho)} + \rho \sum_{j=1}^{\infty} (1-\rho)^{j-1} \sum_{m=1}^{\infty} p_{22}(m)s^{m+j} \\
&= \frac{\rho s}{1-s(1-\rho)} + \frac{\rho s}{1-s(1-\rho)} \sum_{m=1}^{\infty} p_{22}(m)s^m \\
&= \frac{\rho s}{1-s(1-\rho)} \sum_{m=0}^{\infty} p_{22}(m)s^m = \frac{\rho s \psi_{22}(s)}{1-s(1-\rho)}. \tag{3.7}
\end{aligned}$$

Multiplying (3.4) by s^n and summing from $n = 0$ to ∞ , we get

$$\begin{aligned}
\psi_{21}(s) &= \sum_{n=0}^{\infty} p_{21}(n)s^n = \sum_{n=1}^{\infty} p_{21}(n)s^n \\
&= \sum_{n=1}^{\infty} (1-\rho)^{n-1} \rho s^n + \sum_{n=2}^{\infty} \sum_{j=1}^{n-1} (1-\rho)^{j-1} \rho p_{11}(n-j)s^n \\
&= \frac{\rho s}{1-(1-\rho)s} + \rho \sum_{j=1}^{\infty} \sum_{n=j+1}^{\infty} (1-\rho)^{j-1} p_{11}(n-j)s^n \\
&= \frac{\rho s}{1-s(1-\rho)} + \rho \sum_{j=1}^{\infty} (1-\rho)^{j-1} \sum_{m=1}^{\infty} p_{11}(m)s^{m+j}
\end{aligned}$$

$$\begin{aligned}
&= \frac{\rho s}{1-s(1-\rho)} + \frac{\rho s}{1-s(1-\rho)} \sum_{m=1}^{\infty} p_{11}(m) s^m \\
&= \frac{\rho s}{1-s(1-\rho)} \sum_{m=0}^{\infty} p_{11}(m) s^m = \frac{\rho s \psi_{11}(s)}{1-s(1-\rho)}. \tag{3.8}
\end{aligned}$$

Multiplying (3.5) by s^n and summing from $n = 2$ to ∞ , we get

$$\begin{aligned}
\psi_{22}(s) &= \sum_{n=0}^{\infty} p_{22}(n) s^n = \sum_{n=0}^{\infty} (1-\rho)^n s^n + \sum_{n=2}^{\infty} \sum_{j=1}^{n-1} (1-\rho)^{j-1} \rho p_{12}(n-j) s^n \\
&= \frac{1}{1-(1-\rho)s} + \rho \sum_{j=1}^{\infty} (1-\rho)^{j-1} \sum_{m=1}^{\infty} p_{12}(m) s^{m+j} \\
&= \frac{1}{1-(1-\rho)s} + \frac{s \rho \psi_{12}(s)}{1-s(1-\rho)}. \tag{3.9}
\end{aligned}$$

Substituting (3.8) in (3.6) and solving for $\psi_{11}(s)$, we get

$$\psi_{11}(s) = \frac{1}{1-(1-\rho)s} + \frac{s \rho \frac{\rho s \psi_{11}(s)}{1-s(1-\rho)}}{1-s(1-\rho)}$$

and so we get

$$\begin{aligned}
\psi_{11}(s) &= \frac{1-(1-\rho)s}{\{1-s(1-2\rho)\}(1-s)} \\
&= \frac{1}{2} \frac{1}{1-s} + \frac{1}{2} \frac{1}{1-s(1-2\rho)} = \frac{1}{2} \sum_{n=0}^{\infty} \{1 + (1-2\rho)^n\} s^n.
\end{aligned}$$

Consequently, we get

$$p_{11}(t) = \frac{1 + (1-2\rho)^t}{2}, \quad t = 0, 1, 2, \dots \tag{3.10}$$

Substituting (3.6) in (3.8) and solving for $\psi_{21}(s)$, we get

$$\psi_{21}(s) = \frac{s\rho}{1-s(1-\rho)} \left[\frac{1}{1-s(1-\rho)} + \frac{s\rho\psi_{21}(s)}{1-s(1-\rho)} \right].$$

Solving the above equation for $\psi_{21}(s)$, we obtain

$$\begin{aligned} \psi_{21}(s) &= \frac{\rho s}{\{1-s(1-2\rho)\}(1-s)} \\ &= \frac{1}{2} \frac{1}{1-s} - \frac{1}{2} \frac{1}{1-s(1-2\rho)} = \frac{1}{2} \sum_{n=0}^{\infty} \{1-(1-2\rho)^n\} s^n \end{aligned}$$

and hence, we get

$$p_{21}(t) = \frac{1-(1-2\rho)^t}{2}, \quad t = 0, 1, 2, \dots \quad (3.11)$$

Substituting (3.7) in (3.9) and solving for $\psi_{22}(s)$, we get

$$\begin{aligned} \psi_{22}(s) &= \frac{1-(1-\rho)s}{\{1-s(1-2\rho)\}(1-s)} \\ &= \frac{1}{2} \frac{1}{1-s} + \frac{1}{2} \frac{1}{1-s(1-2\rho)} = \frac{1}{2} \sum_{n=0}^{\infty} \{1+(1-2\rho)^n\} s^n \end{aligned}$$

and hence, we get

$$p_{22}(t) = \frac{1+(1-2\rho)^t}{2}, \quad t = 0, 1, 2, \dots \quad (3.12)$$

Substituting (3.9) in (3.7) and solving for $\psi_{12}(s)$, we get

$$\psi_{12}(s) = \frac{\rho s}{\{1-s(1-2\rho)\}(1-s)} = \frac{1}{2} \sum_{n=0}^{\infty} \{1-(1-2\rho)^n\} s^n$$

and hence, we get

$$p_{12}(t) = \frac{1-(1-2\rho)^t}{2}, \quad t = 0, 1, 2, \dots \quad (3.13)$$

Using (3.10) and (3.13), we get

$$\begin{aligned}
 G(s, x; t + 1) &= p_{11}(t)h_1\left(\int_{-\infty}^{\infty} k(x, y)G(s, y; t)dy\right) \\
 &\quad + p_{12}(t)h_2\left(\int_{-\infty}^{\infty} k(x, y)G(s, y; t)dy\right) \\
 &= \frac{1 + (1 - 2\rho)^t}{2} h^{(1)}\left(\int_{-\infty}^{\infty} k(x, y)G(s, y; t)dy\right) \\
 &\quad + \frac{1 - (1 - 2\rho)^t}{2} h^{(2)}\left(\int_{-\infty}^{\infty} k(x, y)G(s, y; t)dy\right).
 \end{aligned}$$

This proves (3.1).

We now proceed to derive several useful statistics from (3.1).

4. The Speed of Invasion

The average cumulative density of invasion is the expected value of $X(t, x)$. We put $a(t, x) = E[X(t, x)]$. To get an integro-difference equation for $a(t, x)$, we differentiate (3.1) with respect to s and put $s = 1$. Then, we get

$$\begin{aligned}
 &a(t + 1, x) \\
 &= \left[\left\{ \frac{1 + (1 - 2\rho)^t}{2} \right\} R_{10} + \left\{ \frac{1 - (1 - 2\rho)^t}{2} \right\} R_{20} \right] \int_{-\infty}^{\infty} k(x, y)a(t, y)dy \\
 &= R_0(t) \int_{-\infty}^{\infty} k(x, y)a(t, y)dy,
 \end{aligned} \tag{4.1}$$

where we have put

$$R_{10} = h^{(1)'}(1), \quad R_{20} = h^{(2)'}(1),$$

$$R_0(t) = \left\{ \frac{1 + (1 - 2\rho)^t}{2} \right\} R_{10} + \left\{ \frac{1 - (1 - 2\rho)^t}{2} \right\} R_{20}.$$

It is important to note that the value of $R_0(t)$ depends on the generation level t . This form of $R_0(t)$ defers from the result of Kot et al. [3]. Following Snyder [10], we proceed to solve equation (4.1) explicitly for the leptokurtic Laplace kernel $k(x, y) = \frac{\alpha}{2} e^{-\alpha|x-y|}$. Equation (4.1) becomes

$$\begin{aligned}
 a(t+1, x) &= R_0(t) \int_{-\infty}^{\infty} \frac{\alpha}{2} e^{-\alpha|x-y|} a(t, y) dy \\
 &\Rightarrow a(t+1, x) \\
 &= R_0(t) \left[\int_{-\infty}^x \frac{\alpha}{2} e^{-\alpha|x-y|} a(t, y) dy + \int_x^{\infty} \frac{\alpha}{2} e^{-\alpha|x-y|} a(t, y) dy \right] \\
 &= R_0(t) \left[\int_{-\infty}^x \frac{\alpha}{2} e^{-\alpha(x-y)} a(t, y) dy + \int_x^{\infty} \frac{\alpha}{2} e^{-\alpha(y-x)} a(t, y) dy \right].
 \end{aligned}$$

Using the trial solution $a(t, x) = e^{-\theta(x-ct)}$, $-\alpha < \theta < \alpha$, equation (4.1) gives

$$\begin{aligned}
 e^{-\theta x + \theta c} &= \frac{\alpha R_0(t)}{2} \left[\int_{-\infty}^x e^{-\alpha(x-y)} e^{-\theta y} dy + \int_x^{\infty} e^{-\alpha(y-x)} e^{-\theta y} dy \right] \\
 &= \frac{\alpha R_0(t)}{2} \left[e^{-\alpha x} \int_{-\infty}^x e^{(-\theta + \alpha)y} dy + e^{\alpha x} \int_x^{\infty} e^{(-\theta - \alpha)y} dy \right] \\
 &= \frac{\alpha R_0(t)}{2} \left[\frac{e^{-\theta x}}{-\theta + \alpha} - \frac{e^{-\theta x}}{-\theta - \alpha} \right]
 \end{aligned}$$

and hence, we get

$$e^{\theta c} = \frac{\alpha R_0(t)}{2} \left[\frac{1}{-\theta + \alpha} - \frac{1}{-\theta - \alpha} \right] = \frac{\alpha^2 R_0(t)}{\alpha^2 - \theta^2}. \quad (4.2)$$

Using the parametric representation for c as

$$c = \frac{2\theta}{\alpha^2 - \theta^2}, \quad (4.3)$$

equation (4.2) gives

$$R_0(t) = \left(1 - \frac{\theta^2}{\alpha^2}\right) e^{2\theta^2/(\alpha^2 - \theta^2)}. \quad (4.4)$$

We now proceed to find the speed of invasion for certain choices of $h_1(s)$, $h_2(s)$, ρ and α .

Illustration 1. Let $h^{(1)}(s) = s^2$, $h^{(2)}(s) = s^2$, $\rho = 0.5$ and $\alpha = 0.5$. Then

$$R_{10} = h^{(1)'}(1) = 2, \quad R_{20} = h^{(2)'}(1) = 2, \quad R_0(t) = \frac{1}{2} R_{10} + \frac{1}{2} R_{20} = 2.$$

Equation (4.4) becomes $2 = (1 - 4\theta^2)e^{8\theta^2/(1-4\theta^2)}$. The above equation is independent of the generation index t . Solving the above equation numerically, we get $\theta = 0.301791$. Substituting in (4.2), we get the speed of invasion for all generations as $c = 3.797971$. This is in fact the result of Snyder [10].

Illustration 2. Let $h^{(1)}(s) = \frac{2}{3}s^2 + \frac{1}{3}s^4$, $h^{(2)}(s) = s^2$, $\rho = 0.4$ and $\alpha = 0.5$. Then

$$R_{10} = h^{(1)'}(1) = \frac{8}{3}, \quad R_{20} = h^{(2)'}(1) = 2.$$

Consequently, we get

$$R_0(t) = \left\{ \frac{1 + (1 - 2\rho)^t}{2} \right\} R_{10} + \left\{ \frac{1 - (1 - 2\rho)^t}{2} \right\} R_{20} = \frac{7}{3} + \frac{1}{3}(0.2)^t.$$

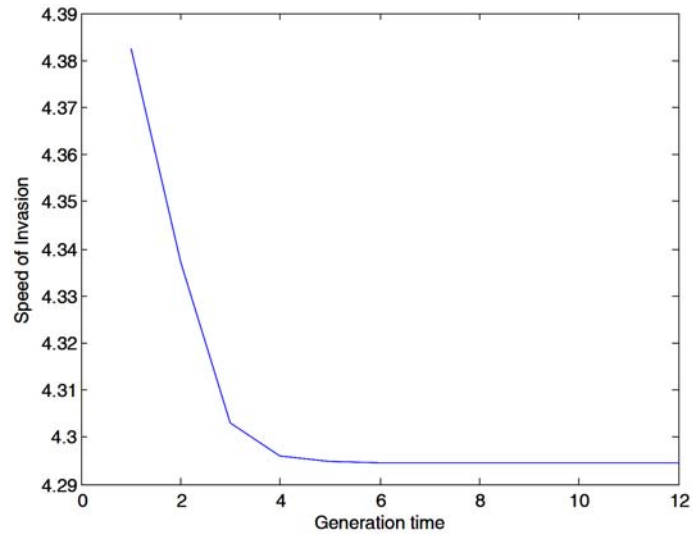
Then equation (4.4) becomes

$$\frac{7}{3} + \frac{1}{3}(0.2)^t = (1 - 4\theta^2)e^{8\theta^2/(1-4\theta^2)}. \quad (4.5)$$

From (4.5), we note that θ is a function of the generation index t and consequently, the invasion speed c is a function of t . Solving (4.5) numerically, we get the following table:

Table 1. Transient speed of invasion in random environment

Generation time	$R_0(t)$	θ	Speed of invasion
1	2.4	0.321424	4.382471
2	2.365333	0.320033	4.337106
3	2.339641	0.318971	4.302923
4	2.334581	0.318758	4.296134
5	2.333582	0.318716	4.294791
6	2.333383	0.318708	4.294523
7	2.333343	0.318706	4.29447
8	2.333335	0.318706	4.294459
9	2.333334	0.318706	4.294457
10	2.333333	0.318706	4.294456
11	2.333333	0.318706	4.294456
12	2.333333	0.318706	4.294456

**Figure 1.** Speed of invasion versus generation time.

We note that the speed of invasion decreases and reaches the steady-state at the tenth generation. The asymptotic speed of invasion is $c = 4.29445$.

Illustration 3. We assume

$$h^{(1)}(s) = \frac{2}{3}s^2 + \frac{1}{3}s^4, \quad h^{(2)}(s) = s^2, \quad \rho = 0.6 \quad \text{and} \quad \alpha = 0.5.$$

Then we obtain

$$R_{10} = h^{(1)'}(1) = \frac{8}{3}, \quad R_{20} = h^{(2)'}(1) = 2, \quad R_0(t) = \frac{7}{3} + \frac{1}{3}(-0.2)^t.$$

Now equation (4.5) becomes

$$\frac{7}{3} + \frac{1}{3}(-0.2)^t = (1 - 4\theta^2)e^{8\theta^2/(1-4\theta^2)}. \quad (4.6)$$

From equation (4.6), we note that θ is a function of the generation index t and consequently, the invasion speed c is a function of t . Solving (4.6) numerically, we get Table 2 and Figure 2.

Table 2. Transient speed of invasion in random environment

Generation time	$R_0(t)$	θ	Speed of invasion
1	2.266667	0.3158	4.203088
2	2.363556	0.31996	4.334756
3	2.327031	0.318439	4.285966
4	2.334574	0.318758	4.296125
5	2.333084	0.318695	4.294121
6	2.333383	0.318708	4.294523
7	2.333323	0.318705	4.294443
8	2.333335	0.318706	4.294459
9	2.333333	0.318706	4.294456
10	2.333333	0.318706	4.294456

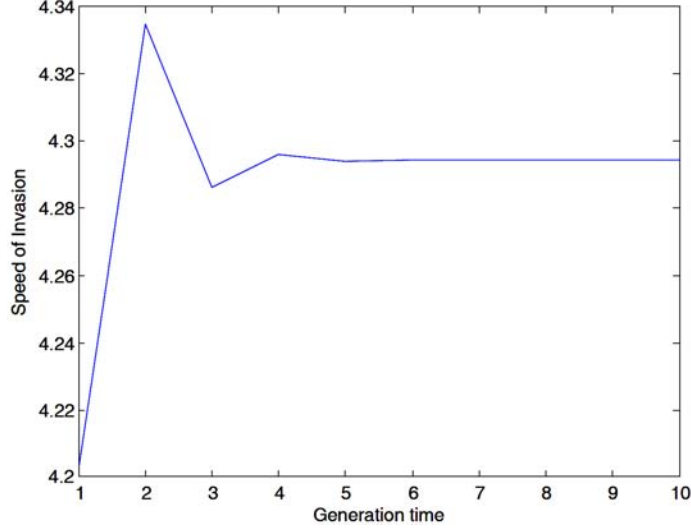


Figure 2. Speed of invasion versus generation time.

In this illustration, the speed of invasion oscillates and then reaches the asymptotic speed 4.294456 at the 9th generation.

5. The Spectral Analysis of Invasion

In this section, we provide a spectral analysis when the spatial distribution kernel is homogeneous, that is $k(x, y) = k(x - y)$. We denote the Fourier transform of $a(t, x)$ as

$$\hat{f}(t, \omega) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} a(t, x) dx.$$

Then equation (4.1) gives

$$\hat{a}(t+1, \omega) = \frac{R_0(t)}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} \int_{-\infty}^{\infty} k(x-y) a(t, y) dy dx. \quad (5.1)$$

We assume that $k(x, y) = k(x - y)$. Interchanging the order of integration in (5.1), we get

$$\begin{aligned}
\hat{a}(t+1, \omega) &= \frac{R_0(t)}{2\pi} \int_{-\infty}^{\infty} a(t, y) \int_{-\infty}^{\infty} e^{i\omega x} k(x-y) dx dy \\
&= \frac{R_0(t)}{2\pi} \int_{-\infty}^{\infty} a(t, y) \int_{-\infty}^{\infty} e^{i\omega x} k(x-y) dx dy \\
&= 2\pi R_0(t) \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega y} a(t, y) dy \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega z} k(z) dz \\
&= 2\pi R_0(t) \hat{a}(t, \omega) \hat{k}(\omega).
\end{aligned}$$

Iterating the above equation, we get

$$\hat{a}(t+1, \omega) = \{2\pi \hat{k}(\omega)\}^{t+1} \prod_{l=0}^t R_0(l) \hat{a}(0, \omega).$$

But we have

$$\begin{aligned}
\hat{a}(0, \omega) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega y} a(0, y) dy = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega y} E[X(0, y)] dy \\
&= \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega y} \delta(y) dy = \frac{1}{2\pi}.
\end{aligned}$$

Consequently, we obtain

$$\hat{a}(t, \omega) = \frac{\{2\pi \hat{k}(\omega)\}^t \prod_{l=0}^{t-1} R_0(l)}{2\pi}. \quad (5.2)$$

Following Snyder [10], suppose that $k(x) = \frac{\alpha}{2} e^{\alpha|x|}$, $-\infty < x < \infty$. Then we have

$$\begin{aligned}
\hat{k}(\omega) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega y} \frac{-\alpha}{2} e^{-\alpha|x|} dx \\
&= \frac{1}{\pi} \int_0^{\infty} \cos(\omega x) \frac{\alpha}{2} e^{-\alpha x} dx = \frac{1}{2\pi} \frac{\alpha^2}{\omega^2 + \alpha^2}.
\end{aligned} \quad (5.3)$$

Substituting (5.3) into (5.2), we get

$$\hat{a}(t, \omega) = \frac{\left\{ 2\pi \times \frac{1}{2\pi} \frac{\alpha^2}{\omega^2 + \alpha^2} \right\}^t \prod_{l=0}^{t-1} R_0(l)}{2\pi} = \frac{\alpha^{2t} \prod_{l=0}^{t-1} R_0(l)}{2\pi(\omega^2 + \alpha^2)^t}. \quad (5.4)$$

Taking Fourier inversion of (5.4), we have

$$a(t, x) = \int_{-\infty}^{\infty} e^{-i\omega x} \frac{\alpha^{2t} \prod_{l=0}^{t-1} R_0(l)}{2\pi(\omega^2 + \alpha^2)^t} d\omega = \frac{\alpha^{2t} \prod_{l=0}^{t-1} R_0(l)}{2\pi} \int_{-\infty}^{\infty} \frac{e^{i\omega x}}{(\omega^2 + \alpha^2)^t} d\omega. \quad (5.5)$$

Using the calculus of residues, we get

$$\int_{-\infty}^{\infty} \frac{e^{i\omega x}}{(\omega^2 + \alpha^2)^t} d\omega = 2\pi i \lim_{z \rightarrow i\alpha} \frac{1}{(t-1)!} \frac{d^{t-1}}{dz^{t-1}} \left[\frac{e^{izx}}{(z + i\alpha)^t} \right]. \quad (5.6)$$

Using the theorem of Leibnitz, equation (5.6) gives

$$\begin{aligned} & \int_{-\infty}^{\infty} \frac{e^{i\omega x}}{(\omega^2 + \alpha^2)^t} d\omega \\ &= \frac{2\pi i}{(t-1)!} \lim_{z \rightarrow i\alpha} \sum_{j=0}^{t-1} \binom{t-1}{j} (e^{izx})_{t-1-j} \{(z + i\alpha)^{-t}\}_j \\ &= \frac{2\pi i}{(t-1)!} \lim_{z \rightarrow i\alpha} \sum_{j=0}^{t-1} \binom{t-1}{j} (ix)^{t-1-j} e^{izx} \left[(-1)^j \prod_{l=0}^{j-1} (t+l) \right] (z + i\alpha)^{-t-j} \\ &= \frac{2\pi i}{(t-1)!} e^{-\alpha x} \left[\sum_{j=0}^{t-1} \binom{t-1}{j} (ix)^{t-1-j} \left[(-1)^j \prod_{l=0}^{j-1} (t+l) \right] (2i\alpha)^{-t-j} \right] \\ &= \frac{2\pi}{(t-1)!} e^{-\alpha x} \sum_{j=0}^{t-1} \binom{t-1}{j} x^{t-1-j} \frac{\prod_{l=0}^{j-1} (t+l)}{(2\alpha)^{t+j}}. \end{aligned} \quad (5.7)$$

Substituting (5.7) into (5.5), we obtain

$$a(t, x) = \frac{\alpha^{2t} \prod_{l=0}^{t-1} R_0(l)}{(t-1)!} e^{-\alpha x} \sum_{j=0}^{t-1} \binom{t-1}{j} x^{t-1-j} \frac{\prod_{l=0}^{j-1} (t+l)}{(2\alpha)^{t+j}}.$$

Next we proceed to investigate the frequency analysis of the spatial covariance of the invasion process. For this, we need the product density functions $p_1(t, x)$ and $p_2(t, x, y)$ which are defined by the equations:

$$p_1(t, x) = \lim_{\Delta \rightarrow 0} \frac{P\{\Omega(t : x, \Delta)\}}{\Delta},$$

$$p_2(t, x, y) = \lim_{\Delta, \Delta' \rightarrow 0} \frac{P\{\Omega(t : x, \Delta; y, \Delta')\}}{\Delta \Delta'},$$

where $\Omega(t : x, \Delta)$ is the event that one individual of t th generation lies in $(x, x + \Delta)$; and $\Omega(t : x, \Delta; y, \Delta')$ is the event that one individual of t th generation lies in $(x, x + \Delta)$ and one individual of t th generation lies in $(y, y + \Delta')$. Then, applying the offspring generation mechanism and the dispersal kernel $k(\xi, \eta)$, we obtain the integro-difference equations for $p_1(t, x)$ and $p_2(t, x, y)$. To derive the integro-difference equation for $p_1(t, x)$, we consider $p_1(t+1, x)$ and observe that the individual at x in the $t+1$ th generation is one of the offspring of an individual of the t th generation. Accordingly, we obtain that the function $p_1(t, x)$ satisfies the integro-difference equation

$$p_1(t+1, x) = p_{11}(t) \int_{-\infty}^{\infty} p_1(t, z) \sum_{j=0}^{\infty} p_j^{(1)} j k(x, z) dz$$

$$+ p_{12}(t) \int_{-\infty}^{\infty} p_1(t, z) \sum_{j=0}^{\infty} p_j^{(2)} j k(x, z) dz$$

$$\begin{aligned}
&= p_{11}(t)R_{10} \int_{-\infty}^{\infty} p_1(t, z)k(x, z)dz \\
&\quad + p_{12}(t)R_{10} \int_{-\infty}^{\infty} p_1(t, z)k(x, z)dz \\
&= \{p_{11}(t)R_{10} + p_{12}(t)R_{20}\} \int_{-\infty}^{\infty} p_1(t, z)k(x, z)dz \\
&= R_0(t) \int_{-\infty}^{\infty} p_1(t, z)k(x, z)dz. \tag{5.8}
\end{aligned}$$

To derive the integro-difference equation for $p_2(t, x, y)$, we consider $p_2(t+1, x, y)$ and observe that the two individuals at x and y of the $t+1$ th generation are due to the same parent of the t th generation or due to different parents of the t th generation. Accordingly, we obtain that the function $p_2(t, x, y)$ satisfies the integro-difference equation

$$\begin{aligned}
p_2(t+1, x, y) &= \int_{-\infty}^{\infty} p_1(t, z) \left\{ p_{11}(t) \sum_{j=0}^{\infty} p_j^{(1)} j(j-1) \right. \\
&\quad \left. + p_{12}(t) \sum_{j=0}^{\infty} p_j^{(2)} j(j-1) \right\} k(x, z)k(y, z)dz \\
&\quad + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{u \neq v} p_2(t, u, v) \left\{ p_{11}(t) \sum_{j,l=0}^{\infty} p_j^{(1)} j p_l^{(1)} \right. \\
&\quad \left. + p_{12}(t) \sum_{j,l=0}^{\infty} p_j^{(2)} j p_l^{(2)} \right\} k(x, u)k(y, v)dudv.
\end{aligned}$$

In the above equation, we note that

$$R_{10} = h^{(1)'}(1) = \sum_{j=0}^{\infty} p_j^{(1)} j,$$

$$R_{20} = h^{(2)'}(1) = \sum_{j=0}^{\infty} p_j^{(2)} l;$$

$$m_2^{(1)} = h^{(1)''}(1) = \sum_{j=0}^{\infty} p_j^{(1)} j(j-1),$$

$$m_2^{(2)} = h^{(2)''}(1) = \sum_{j=0}^{\infty} p_j^{(2)} j(j-1).$$

Consequently, the above equation becomes

$$\begin{aligned} & p_2(t+1, x, y) \\ &= \int_{-\infty}^{\infty} p_1(t, z) \{p_{11}(t)m_2^{(1)} + p_{12}(t)m_2^{(2)}\} k(x, z)k(y, z) dz \\ &+ \int_{-\infty}^{\infty} \int_{-\infty, u \neq v}^{\infty} p_2(t, u, v) \{p_{11}(t)R_{10}^2 + p_{12}(t)R_{20}^2\} k(x, u)k(y, v) dudv \\ &= a(t) \int_{-\infty}^{\infty} p_1(t, z) k(x, z)k(y, z) dz \\ &+ b(t) \int_{-\infty}^{\infty} \int_{-\infty, u \neq v}^{\infty} p_2(t, u, v) k(x, u)k(y, v) dudv, \end{aligned} \quad (5.9)$$

where we have put $a(t) = p_{11}(t)m_2^{(1)} + p_{12}(t)m_2^{(2)}$ and $b(t) = p_{11}(t)R_{10}^2 + p_{12}(t)R_{20}^2$. Putting $h^{(1)}(s) = h^{(2)}(s)$, we get back the same equation as in Lewis and Pacala [5]. To solve equations (5.8) and (5.9), we assume $k(u, v) = k(u - v)$ and apply the Fourier transform and double Fourier transform, respectively, as defined by

$$\hat{f}(\omega) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} f(x) dx,$$

$$\hat{f}(\omega_1, \omega_2) = \frac{1}{4\pi^2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{i\omega_1 x} e^{i\omega_2 y} f(x, y) dx dy.$$

By taking Fourier transform of (5.8), we obtain

$$\begin{aligned}
\hat{p}_1(t+1, \omega) &= R_0(t) \int_{-\infty}^{\infty} p_1(t, z) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} k(x-z) dx \right) dz \\
&= R_0(t) \int_{-\infty}^{\infty} p_1(t, z) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega(\xi+z)} k(\xi) d\xi \right) dz \\
&= 2\pi R_0(t) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega z} p_1(t, z) dz \right) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega \xi} k(\xi) d\xi \right) \\
&= 2\pi R_0(t) \hat{p}_1(t, \omega) \hat{k}(\omega). \tag{5.10}
\end{aligned}$$

Similarly, taking double Fourier transform on both sides of (5.9), we get

$$\begin{aligned}
&\hat{p}_2(t+1, \omega_1, \omega_2) \\
&= a(t) \int_{-\infty}^{\infty} p_1(t, z) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_1 x} k(x-z) dx \right) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_2 y} k(y-z) dy \right) dz \\
&\quad + b(t) \int_{-\infty}^{\infty} \int_{-\infty, u \neq v}^{\infty} p_2(t, u, v) \frac{1}{2\pi} \left(\int_{-\infty}^{\infty} e^{i\omega_1 x} k(x-u) dx \right) \\
&\quad \times \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_2 y} k(y-v) dy \right) dudv \\
&= a(t) \int_{-\infty}^{\infty} p_1(t, z) \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_1(\xi+z)} k(\xi) d\xi \right) \\
&\quad \times \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_2(\eta+z)} k(\eta) d\eta \right) dz \\
&\quad + b(t) \int_{-\infty}^{\infty} \int_{-\infty, u \neq v}^{\infty} p_2(t, u, v) \frac{1}{2\pi} \left(\int_{-\infty}^{\infty} e^{i\omega_1(\xi+u)} k(\xi) d\xi \right) \\
&\quad \times \left(\frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega_2(\eta+v)} k(\eta) d\eta \right) dudv
\end{aligned}$$

$$= 2\pi a(t) \hat{p}_1(t, \omega_1 + \omega_2) \hat{k}(\omega_1) \hat{k}(\omega_2) + 4\pi^2 b(t) \hat{p}_2(t, \omega_1, \omega_2) \hat{k}(\omega_1) \hat{k}(\omega_2). \quad (5.11)$$

Solving equation (5.10), we get

$$\hat{p}_1(t, \omega) = (2\pi)^t \prod_{j=0}^{t-1} R_0(j) \{\hat{k}(\omega)\}^t \hat{p}_1(0, \omega). \quad (5.12)$$

But, we have

$$\hat{p}_1(0, \omega) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} p_1(0, x) dx = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{i\omega x} \delta(x) dx = \frac{1}{2\pi}.$$

Consequently, equation (5.12) gives

$$\hat{p}_1(t, \omega) = \frac{(2\pi)^t \prod_{j=0}^{t-1} R_0(j) \{\hat{k}(\omega)\}^t}{2\pi}. \quad (5.13)$$

Solving equation (5.11), we get

$$\begin{aligned} \hat{p}_2(t, \omega_1, \omega_2) &= 2\pi \hat{k}(\omega_1) \hat{k}(\omega_2) a(t-1) \hat{p}_1(t-1, \omega_1 + \omega_2) \\ &+ \frac{1}{2\pi} \sum_{j=1}^{t-1} \{4\pi^2 \hat{k}(\omega_1) \hat{k}(\omega_2)\}^{j+1} a(t-1-j) \\ &\times \prod_{l=0}^{j-1} b(t-1-l) \hat{p}_1(t-1-j, \omega_1 + \omega_2) \\ &+ \sum_{j=1}^{t-1} \{4\pi^2 \hat{k}(\omega_1) \hat{k}(\omega_2) b(t-1-j)\} \hat{p}_2(0, \omega_1, \omega_2). \end{aligned} \quad (5.14)$$

Since $p_1(0, x) = \delta(x)$, $p_2(0, x, y) = 0$, $x \neq y$, we get $\hat{p}_1(0, \omega) = \frac{1}{2\pi}$ and

$\hat{p}_2(0, \omega_1, \omega_2) = 0$. Consequently, (5.14) gives

$$\begin{aligned}
\hat{p}_2(t, \omega_1, \omega_2) &= 2\pi\hat{k}(\omega_1)\hat{k}(\omega_2)a(t-1)\hat{p}_1(t-1, \omega_1 + \omega_2) \\
&+ \frac{1}{2\pi} \sum_{j=1}^{t-1} \{4\pi^2\hat{k}(\omega_1)\hat{k}(\omega_2)\}^{j+1} a(t-1-j) \\
&\times \prod_{l=0}^{j-1} b(t-1-l)\hat{p}_1(t-1-j, \omega_1 + \omega_2). \quad (5.15)
\end{aligned}$$

Let us consider the particular case, $h^{(j)}(s) = e^{\lambda_j(s-1)}$, $j = 1, 2$. Then, we have

$$R_{10} = \lambda_1, \quad R_{20} = \lambda_2, \quad m_2^{(1)} = \lambda_1^2, \quad m_2^{(2)} = \lambda_2^2$$

so that $a(t) = p_{11}(t)\lambda_1^2 + p_{12}(t)\lambda_2^2 = b(t)$. Consequently, equation (5.15) gives

$$\begin{aligned}
&\hat{p}_2(t, \omega_1, \omega_2) \\
&= \frac{1}{2\pi} \sum_{j=1}^{t-1} \{4\pi^2\hat{k}(\omega_1)\hat{k}(\omega_2)\}^{j+1} \prod_{l=0}^j a(t-1-l)\hat{p}_1(t-1-j, \omega_1 + \omega_2).
\end{aligned}$$

6. Discussion and Conclusion

From the understanding of ecological and evolutionary theory, our ability to predict accurately future extinction events is limited. The total number of recent extinctions is not completely known. The present communication is towards estimating the effect of invasion of species in a lake environment. Figure 1 and Figure 2 show the effect of invasion. Both graphs indicate a general saturation after some generation time. As per Island Biography Theory (IBT), we can attribute this phenomenon to “extinctions based saturation.” This means that at the saturation point, the addition of new colonizing species will result in the local extinction. But there is different view point if we consider stochastic niche theory. According to this theory, the total number of species in a place, in the present case a lake, could be

maintained by suppression of colonization which is indicated by our stochastic model because of the inhibitive effect of species already present to the invading species. This is understandable from the fact that there is resource constraint and the available resource is to be partitioned among the total species and thus there is an inhibitive effect. But as per IBT, continued addition of exotic species should result in the extinction of native species. The rate of extinction will increase if the rate of colonization increases. If this is accepted, then the number of native plant extinctions can be understood. But as per colonization based saturations, the existing species should get benefits if the invading species judiciously and efficiently adjust the resources. From the analysis of the results of extinction patterns over the last 500 years, the majority of documented extinctions have taken place on islands and not on main lands and this goes well with colonization based saturation. This is true for both terrestrial vertebrates and plants. On the other hand, extinctions facilitated by exotic species which are considered to be one of the factors contributing to the native species extinction. Among the 204 vertebrates species that are reported to have become extinct, predation (human hunting, carnivorous activity, death due to infectious diseases) is reported to be the main reason.

The above can be viewed from a kinetic angle. There is a competition between coarsening dynamics and reactive stationary state. There is a similar situation in kinetics. Depending on mutation rate, equilibrium and non-equilibrium process may result. Depending on mutations to predator and on mutations to the prey, the shift of the equilibrium occurs. The present work suggests that invasion speed is rather slow compared to traditional methods. This may be due to the effect of demographic stochasticity and generally density-dependent births will show the wave. Lewis [4] explored the speed rate for a particular nonlinear stochastic invasion model which is generally a macroscopic model. In the present work, microscopic invasions have been considered in terms of demographic stochasticity and the individuals are supposed to interact in pairs and not in clusters. Further, the present work clearly obtains the upper bound speed that would have been predicted by the deterministic model. If the stochasticity difference is larger, then the

differences in speeds also would have been wider. Generally higher carrying capacity or mutation rate will make anomalous speed. In the present work, moderate carrying capacity and moderate mutation rates have been assumed. Hence the invasion speed attains constant velocity with generation time as indicated in Figure 1 and Figure 2.

All along we have discussed for the growth rate of morphs with generation time. This may not be constant, as we have achieved in our present model, if the morphs differ in both, then dispersal ability and the invasion speed can be faster than the speed of either morph on its own. Our model will be valid in the case of carrying capacity is high enough or when the mutation rates between morphs is big. We have shown that demographic stochasticity can slow down invasions. But this is dependent on the carrying capacity and the mutation rate. We will take these aspects in our future model in motivating further research into understanding the difference between deterministic and stochastic models and the implications that anomalous speeds have for predicting the rate of range expansions.

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