Contents

Spatial Dynamics in Ecology

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1. Introduction

The purpose of this chapter is to introduce the student to the methods of spatial dynamics in biology. They are to form the building blocks for later lectures in the PCMI series. The approach taken here is to introduce some well known ideas and methods in spatial dynamics in the context of a new problem in mathematical biology. Many of the general results here can be found in the excellent texts by Fife [**7**], Kot [**10**], and Okubo [**13**], as well as in the new text by de Vries et al [**6**].

The problem that provides the context for this chapter is called the *drift paradox* in stream ecology [**12**]. The paradox can be summarized by a question. Why can populations persist in streams when they are being constantly washed downstream? While the problem has been recognized for half a century, the application of methods of spatial dynamics to the problem has occurred in the last five years, starting with the work of Speirs and Gurney [**15**]. Speirs and Gurney modeled the drift paradox using partial differential equations. The analysis of the equations was then used, for example, to show why invasive zebra mussels *Dreissena polymorpha* cannot persist in certain US rivers, or why stone flies can persist, but fish cannot persist in certain creeks in southeast UK. Here the mathematical analysis allows us to link persistence of species to environmental conditions in streams and rivers.

Even though the models discussed here have been used to understand specific stream ecosystems, the models themselves are simple, and leave out many biologically relevant factors. The primary motivation is to use the model to understand the essential processes governing species persistence and spread. Extensions of Speirs and Gurney's work to more realistic stream ecosystems have been made by Pachepsky et al [**14**] and Lutscher et al [**11**]. However, we will stick to the simplest versions of the models for the purposes of this chapter.

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Thanks to Caspar Williams for help in preparing some of the figures. The notes are partially based on Chapters 4 and 5 of de Vries, Hillen, Lewis, Müller, and Schönfisch [**6**].

2. Deriving the model

We first focus on deriving a model that includes the relevant spatial and growth dynamics. This model takes the form of a reaction-advection-diffusion model. The 'reaction' describes birth and death dynamics, the 'advection' describes drift in the stream, and the 'diffusion' describes random movement in the stream.

There are two fundamental ways to derive the model. The first is via a *conservation law.* This approach comes from mathematical physics. The conservation equation tracks the density of individuals over time and space by specifying forms for the 'reaction', which describes population growth, and for the flux of individuals, which describes drift and random motion.

The second approach comes from stochastic processes. If we ignore birth and death dynamics for now, the location of an individual is a random variable, indexed by time, (i.e., a stochastic process). This random variable has an associated probability density function. The probability density function changes with time, as the individual executes steps in a biased random walk. The resulting model is an advection-diffusion equation referred to variously as the Fokker-Planck equation, or the forward Kolmogorov equation.

2.1. Conservation law derivation

Assume a population with density $u(\mathbf{x},t)$ is living and moving in a given region. To describe movement, we introduce another dependent quantity, the population flux, $\mathbf{J}(\mathbf{x},t) \in \mathbb{R}^n$, where n is the space dimension. At each location $\mathbf{x}$ and at each time t, the flux $\mathbf{J}(\mathbf{x},t)$ is a vector which points in the direction of movement at that location. Its units are density times velocity, and its magnitude, $|\mathbf{J}(\mathbf{x},t)|$, is proportional to the amount of particles which flow in that direction per unit time.

We assume that the population density and the flux are smooth functions of space and time. We consider a test volume Ω with boundary Γ and we balance the fluxes inward and outward on Ω through Γ (see Figure 1). In words,

Change of u in Ω = flux into Ω + change due to birth, death, interactions.

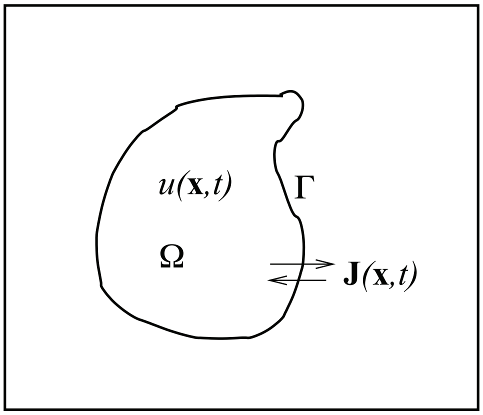

FIGURE 1. Sketch of a test volume Ω with boundary Γ, population density $u(\mathbf{x},t)$, and flux $\mathbf{J}(\mathbf{x},t)$ through the boundary.

Written in mathematical terms, this means

$$\frac{d}{dt}\int_\Omega u(\mathbf{x},t)dV = -\int_\Gamma \mathbf{J}(\mathbf{x},t)\cdot\mathbf{n}\,dS + \int_\Omega f(u(x,t))dV,$$

where $\mathbf{n}$ is the outwardly oriented unit vector normal to Γ.

We use the Divergence Theorem

$$\int_\Gamma \mathbf{J}(\mathbf{x},t)\cdot\mathbf{n}\,dS = \int_\Omega \nabla\cdot\mathbf{J}(\mathbf{x},t)dV,$$

and we get

$$\int_\Omega \left(\frac{\partial}{\partial t}u - f(u) + \nabla\cdot\mathbf{J}\right)dV = 0.$$

The above relation is satisfied in each test volume Ω. Then it follows that

$$\frac{\partial}{\partial t}u - f(u) + \nabla\cdot\mathbf{J} = 0. \tag{1}$$

Next, we need an expression of the flux in terms of the population density. Simple diffusive flux arises from Fick's second law[1]

$$\mathbf{J} = -D\nabla u. \tag{2}$$

This law assumes that the flux $\mathbf{J}$ is proportional to the negative gradient of the density of individuals. Note that, for the units to match in (2), the diffusion coefficient D must have units space^{2}time^{-1}.

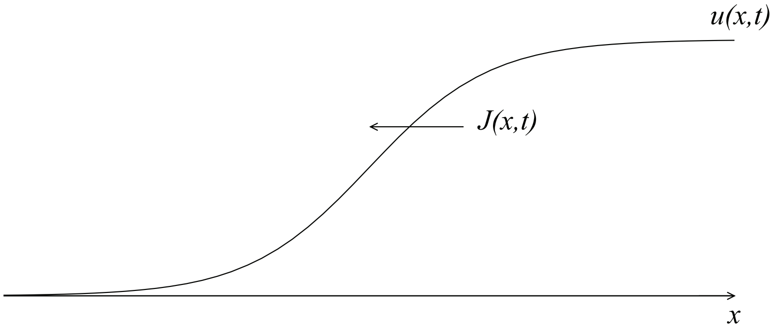

FIGURE 2. Schematic of Fick's second law. A positive gradient of u gives rise to a negative flux J.

In Figure 2, we show a positive gradient of u ($\frac{\partial}{\partial x}u(x,t) > 0$). The flux points to the left, tending to equilibrate high and low levels of u. If there is also advection (drift) with velocity $\mathbf{v}$ then Fick's law is modified to

$$\mathbf{J} = -D\nabla u + \mathbf{v}u. \tag{3}$$

If we combine the balance law (1) with the general version of Fick's law (3), we get a *reaction-advection-diffusion equation*. When the diffusion coefficient D is constant this equation is

$$\frac{\partial u}{\partial t} + \nabla\cdot(\mathbf{v}u) = D\Delta u + f(u), \tag{4}$$

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[1] In the interpretation of heat transport, this law is known as *Fourier's Law*.

where the Laplacian Δu is defined as

$$\Delta u(x,t) = \frac{\partial^2}{\partial x_1^2} u(x,t) + \cdots + \frac{\partial^2}{\partial x_n^2} u(x,t), \quad x = (x_1, \ldots, x_n) \in \mathbb{R}^n.$$

If there are no growth dynamics ($f = 0$), and there is no advection ($\mathbf{v} = 0$) then equation (4) is simply the *diffusion equation* or *heat equation*.

2.2. The Fokker-Planck equation

Most living organisms move in space. Given that we have some information about how an organism moves over short time scales, can we determine where it is likely to be over long time scales? If movement rules are simple, mathematical models can be used to translate the movement rules into equations. As we will show in this section, analysis of the resulting equations yields an equation for a probability density function that can be used to track the changing location of the organism over time.

We consider an individual executing a random walk in one-dimensional space. At each time-step, the individual either jumps to the right or left, and its new position is determined by its current position plus a random increment to the left or right. This is called a one-step *Markov process*, because it is a stochastic process which requires only the knowledge of its current location, plus the random increment, to determine the next position. The precise path taken to get to the current location plays no role in determining future positions. A very readable introduction to stochastic processes is Allen [**2**].

We now consider the probability density function (PDF) for the location of the individual, released at location $x = 0$ at time $t = 0$, for times $t > 0$. Rather than calculating the probability density directly, we show that the PDF satisfies a diffusion-advection equation called the Fokker-Planck equation. As we will show in the subsequent section, when the Fokker-Planck equation comes from a simple movement model, it can be directly solved.

We start with a *master equation* describing possible locations of the individual from one time step to the next. Let $X(t)$ be a stochastic process describing the location of an individual at time t, which is released at location $x = 0$ at time $= 0$ ($X(0) = 0$). We define a time-dependent probability density function $p(x,t)$ and small space interval λ, such that $p(x,t)\lambda =$ probability an individual released at $x = 0$ and time $= 0$ is between x and $x + \lambda$ at time t.

We start by assuming that the random walk is unbiased, with individuals moving at every time step. This means that the probability of jumping to the right, R, or left, L in a given time step is one half. The *master equation* which describes movement between points situated distance λ apart is

$$p(x, t+\tau) = \frac{1}{2}\, p(x-\lambda, t) + \frac{1}{2}\, p(x+\lambda, t) \tag{5}$$

(see Figure 3).

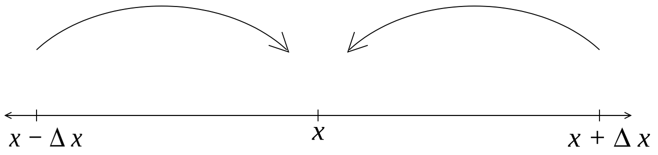

Figure 3. Movement on the lattice giving rise to the diffusion equation. Here an individual arriving at x can come from locations $x - \Delta x$ and $x + \Delta x$, where $\Delta x = \lambda$ in equation (5).

Expanding the Taylor series gives:

$$\begin{aligned} p(x,t) \quad &+ \quad \tau \frac{\partial p}{\partial t}(x,t) + \frac{(\tau)^2}{2}\frac{\partial^2 p}{\partial t^2}(x,t) + \text{h.o.t.} \\ &= \quad \tfrac{1}{2} \quad \Bigg\{ p(x,t) - \lambda \frac{\partial p}{\partial x}(x,t) + \frac{(\lambda)^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t) + \text{h.o.t.} \\ &\qquad + \quad p(x,t) + \lambda \frac{\partial p}{\partial x}(x,t) + \frac{(\lambda)^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t) + \text{h.o.t.} \Bigg\}, \end{aligned}$$

where h.o.t. indicates higher order terms in the Taylor series. The above equation can be approximated by dropping the higher order terms and reorganizing to yield

$$\frac{\partial p}{\partial t} + \frac{\tau}{2}\,\frac{\partial^2 p}{\partial t^2} = \frac{(\lambda)^2}{2\tau}\,\frac{\partial^2 p}{\partial x^2}.$$

Taking the limit as $\lambda, \tau \to 0$ so that $\frac{(\lambda)^2}{2\tau} \to D$ yields the diffusion equation:

$$\frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2}. \tag{6}$$

A slight bias in the movement direction ($R = 0.5 + \gamma\lambda$, $L = 0.5 - \gamma\lambda$) yields the advection-diffusion equation

$$\frac{\partial p}{\partial t} + v\frac{\partial p}{\partial x} = D\frac{\partial^2 p}{\partial x^2}, \tag{7}$$

where $\frac{\gamma(\lambda)^2}{2\tau} \to v$. The biased random walk model can be extended to higher spatial dimensions to yield the n-dimensional advection diffusion equation ((4) with $f = 0$).

Exercise (Random walk derivation of a diffusion-advection equation)

Describe, by means of a master equation, a random walk with movement to nearest neighbors on a 2D lattice with spacing λ and time steps of size τ. Denote L, R, U and V to be the probability of moving to the left, right up or down, respectively. Assume that $L = 0.25 - \lambda\gamma_1$, $R = 0.25 + \lambda\gamma_1$, $U = 0.25 + \lambda\gamma_2$ and $V = 0.25 - \lambda\gamma_2$. Derive a diffusion-advection equation

$$\frac{\partial p}{\partial t} + \mathbf{v} \cdot \nabla p = \nabla \cdot D \nabla p$$

by taking the appropriate diffusion limit of the random walk. Here $\mathbf{v}$ is an advection vector which you should describe in terms of γ_1 and γ_2.

When the probabilities of jumping to right and left depend on spatial location a more complex form of the Fokker Planck equation arises.

Exercise (Spatially varying diffusion model)

Using Taylor Series and the diffusion limit, derive an equation for $\partial p/\partial t$ where

(a) $p(x,t+\tau) = \alpha(x-\lambda)p(x-\lambda,t) + N(x)p(x,t) + \alpha(x+\lambda)p(x+\lambda,t)$ and
(b) $p(x,t+\tau) = \alpha(x-\lambda/2)p(x-\lambda,t) + N(x)p(x,t) + \alpha(x+\lambda/2)p(x+\lambda,t)$.

In the first model, $2\alpha(x)$ and $N(x)$ describe the probabilities of leaving the site or staying at the site. In the second model $\alpha(x-\lambda/2)+\alpha(x+\lambda/2)$ and $N(x)$ describe the probabilities of leaving a site or staying at a site, respectively. Note that $N(x)+2\alpha(x) = 1$ in the first model and $N(x)+\alpha(x-\lambda/2)+\alpha(x+\lambda/2) = 1$ in the second model. Show that the first problem can be written in the form

$$\frac{\partial p}{\partial t} = \frac{\partial^2}{\partial x^2}\left\{A(x)p\right\},$$

where $A(x)$ is a function you should determine. (HINT: when deriving Taylor expansions it may be easiest to expand the product of two functions.) Show that the second problem can be written in the form

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x}\left\{B(x)\frac{\partial p}{\partial x}\right\},$$

where $B(x)$ is a function you should determine. Compare and contrast the assumptions for the two models and the resulting equations for p_t. Show that the difference between the two models can be expressed as an advection term that appears in one model but not the other. For further reading on this see Aronson [**3**].

So far we have derived the diffusion-advection equation two different ways, first from a conservation law, and second from random walk. If we are to calculate the density of individuals (or, alternately, the probability density function for a single individual) we must solve this equation. This is what we consider in the next section.

2.3. Fundamental solution to the diffusion equation

The fundamental solution is a particular solution of the diffusion equation (equation (6), or equivalently, equation (4) with $f = 0$ and $\mathbf{v} = 0$), that can be used to find other solutions by convolution (see, for example, Britton [**5**]).

The *fundamental solution* can be interpreted as the solution to the Fokker-Planck equation (6) for an individual which starts at the location $x = 0$ at time $t = 0$.

To denote this single individual whose initial location is known precisely we use a *δ-distribution* $\delta_0(x)$. The δ-distribution denotes a unit impulse, centered at $x = 0$. Mathematically, it is defined by its action on smooth functions. If $h(x)$ is a smooth function, then $\delta_0(x)$ is the one and only object which satisfies

$$\int_R \delta_0(x)h(x)dx = h(0)$$

and

$$\int_R \delta_0(x)dx = 1.$$

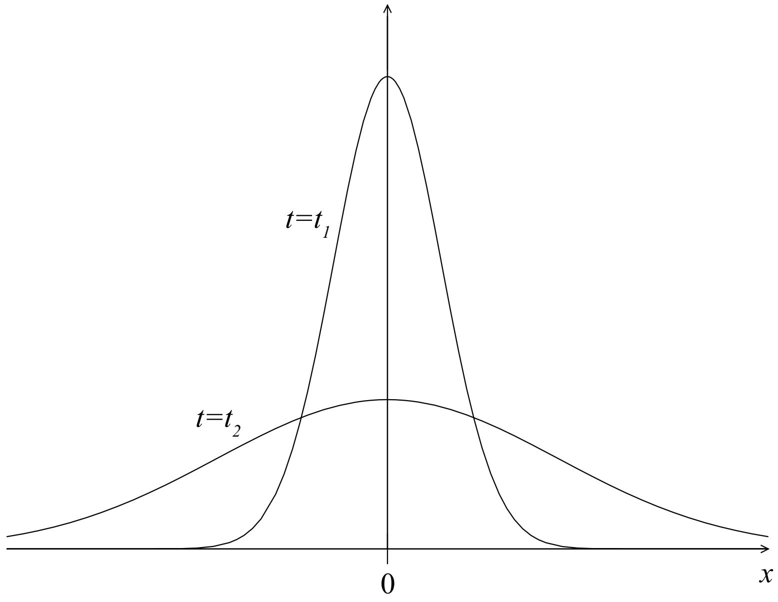

FIGURE 4. Solutions of the diffusion equation (6) are given for three time values, $t = 0$, $t = t_1 > 0$, and $t = t_2 > t_1$.

Consider the *initial-value problem* for a particle which diffuses in one dimension and starts with certainty at 0:

$$w_t = Dw_{xx}, \quad w(x, 0) = \delta_0(x). \tag{8}$$

The *fundamental solution* (in one dimension) is

$$w(x, t) = \frac{1}{2\sqrt{\pi D t}} e^{-\frac{x^2}{4Dt}}. \tag{9}$$

This can be found by using Fourier Transform methods [**9**].

Exercise (Fundamental solution)

(a) Verify that the function

$$w(x, t) = \frac{1}{2\sqrt{\pi D t}}\, e^{-\frac{x^2}{4Dt}}$$

satisfies the diffusion equation $w_t = Dw_{xx}$.

(b) Derive the fundamental solution to the diffusion-advection equation $u_t + vu_x = Du_{xx}$.

In Figure 4, we show this solution for time steps $t = 0$, $t = t_1 > 0$, $t = t_2 > t_1$, and $D = 1$. As time increases, the variance of the Gaussian increases, and hence the location of the individual becomes less certain.

Although the initial condition is not continuous, the solution (9) is continuous for all $t > 0$. In fact, it is infinitely often continuously differentiable, a property which is known as the *regularizing* property of the diffusion equation.

If we study the diffusion equation with a general initial condition,

$$u_t = Du_{xx}, \quad u(x,0) = h(x), \tag{10}$$

then the solution can be found by convolution with w:

$$u(x,t) = (h * w(\cdot,t))(x),$$

where the convolution integral is given by

$$(h * w(\cdot,t))(x) = \int_{-\infty}^{\infty} h(y)\, w(x-y,t)\, dy \tag{11}$$

$$= \frac{1}{2\sqrt{\pi D t}} \int_{-\infty}^{\infty} h(y) e^{-\frac{(x-y)^2}{4Dt}}\, dy. \tag{12}$$

This convolution of the fundamental solution with initial conditions works also for general linear operators, including the diffusion advection equation (7).

3. Population spread

One measure of whether a population can persist in a stream is whether it will invade spatially when introduced into localized region of the stream. We initially analyze a very long (in fact, infinitely long) stream, so there are no losses at upstream and downstream boundaries. These kinds of boundary losses are considered in the subsequent section. We also initially choose the drift term (advection velocity) to be zero. While this is clearly an unreasonable assumption, we make the assumption only for clarity of exposition. The analysis of the zero advection case can be easily extended to include advection and we do this later in the section.

We write our reaction-diffusion model for growth and dispersal in the stream in one spatial dimension. Here x is the distance down river and $n(x,t)$ is the density of individuals in the stream. Random motion, coupled to growth, yields

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + f(n), \tag{13}$$

Here typical growth dynamics are logistic growth

$$f(n) = rn\left(1 - \frac{n}{K}\right). \tag{14}$$

However, some populations have a reduced per capita growth rate at low densities, so on average they cannot replace themselves when densities are low. This is referred to as an 'Allee effect' in honor of Allee, a biologist from the first part of the 20th century who deduced that these effects may be important in the dynamics of populations (Allee [**1**]). The bistable growth function

$$f(n) = rn\left(1 - \frac{n}{K}\right)\left(\frac{n-C}{K}\right) \tag{15}$$

is an appropriate model for the Allee effect.

We can simplify our model by rescaling population density by the carrying capacity, and time and space by characteristic time and length scales.

$$u = \frac{n}{K}, \quad t^* = rt, \quad x^* = \sqrt{\frac{r}{D}}x.$$

This rescaling renders our new quantities u, t^* and x^* dimensionless. We now drop the asterisks on t and x for notational simplicity. Our new equation is

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + g(u), \tag{16}$$

where $g(u) = u(1-u)$ for logistic growth and $g(u) = u(1-u)(u-a)$ for bistable growth.

Our first step in analyzing population spread is to consider travelling wave solutions of (16). Travelling wave solutions are translationally invariant solutions which move with a fixed profile and constant speed.

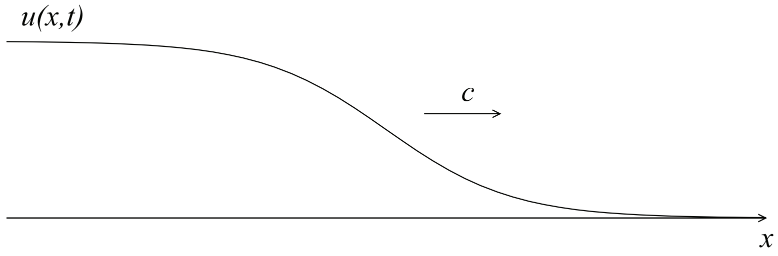

Figure 5. A typical invasion travelling wave.

In particular, we seek solutions $u(x,t)$ that have the form shown in Figure 5, joining the extinction steady state $u = 0$ to the carrying capacity steady state $u = 1$, and moving with constant speed c. A solution of this type can be expressed as

$$u(x,t) = U(x - ct).$$

The function $U(x - ct)$ is the function $U(x)$ shifted to the right by ct, see Figure 6. The parameter c is the *wave speed*, the new variable $z = x - ct$ is called the *wave variable*, and the function $U(z)$ is called the *wave profile*.

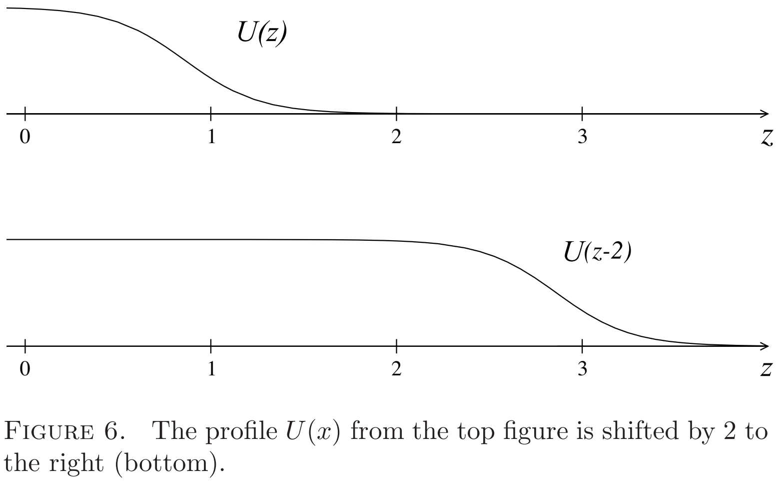

Figure 6. The profile $U(x)$ from the top figure is shifted by 2 to the right (bottom).

The travelling wave ansatz, with boundary conditions is

$$u(x,t) = U(x - ct), \quad U(-\infty) = 1, \quad U(+\infty) = 0, \tag{17}$$

For $x \to -\infty$, the population has already grown to its carrying capacity (1 in this case), and for $x \to +\infty$, the population has not yet arrived.

From (17), we obtain

$$\frac{\partial}{\partial t}u(x,t) = -cU', \quad \frac{\partial^2}{\partial x^2}u(x,t) = U'',$$

and (16) reduces to the following ordinary differential equation f or $U(z)$

$$-cU' = U'' + g(U) \tag{18}$$

To allow analysis in the phase plane, we introduce a new variable, $V = U'$, and write (18) as a 2×2 system

$$\begin{aligned} U' &= V, \\ V' &= -cV - g(U) \end{aligned} \tag{19}$$

Before doing further analysis, we need to specify the dynamics $g(u)$ in equation (16) precisely. We consider the case with logistic growth so that $g(U) = U(1-U)$. The model (16) with logistic growth is referred to as Fisher's equation in honor of R.A. Fisher, a quantitative geneticist who used this equation to study the spatial spread of an advantageous gene into a new environment (Fisher [**8**]). The analysis of the bistable case is left as an exercise (below).

The equilibria of (19) are $P_1 = (0,0)$ and $P_2 = (1,0)$. Using the linearization, we find that the point $P_1 = (0,0)$ is stable for $c > 0$. It is a stable spiral for $c < 2$, and a stable node for $c \geq 2$. The point $P_2 = (1,0)$ is always a saddle.

Recall that the boundary conditions for the wave profile are $U(-\infty) = 1$ and $U(+\infty) = 0$. Moreover, from the form of U as shown in Figure 7, it is clear that $V(-\infty) = V(+\infty) = 0$. In the phase portrait of system (19), we must find a connection from the saddle $(1,0)$ to the stable point $(0,0)$. We show these connections for $c < 2$ in Figure 8 (saddle-focus), and for $c \geq 2$ in Figure 9 (saddle-node).

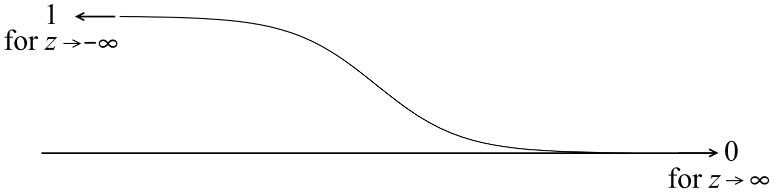

FIGURE 7. The travelling wave as a function of the wave variable z.

Exercise (Phase plane analysis for the bistable travelling wave)

Analyze the bistable travelling wave problem in the phase plane. Show that a heteroclinic connection from $U = 1$ to $U = 0$ yields a saddle-saddle connection in the phase plane.

The function U is the profile of the population density; hence it must be non-negative. Thus solutions for $c < 2$ are not biologically relevant. (Nor are they

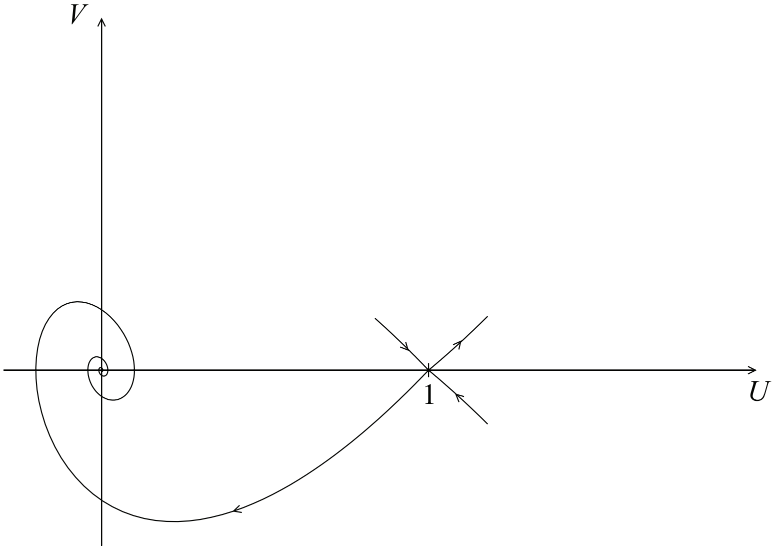

FIGURE 8. Heteroclinic connection from the saddle at $(1,0)$ to the stable spiral at $(0,0)$. Here $\mu = D = 1$ and $c < 2$. There is no non-negative travelling wave.

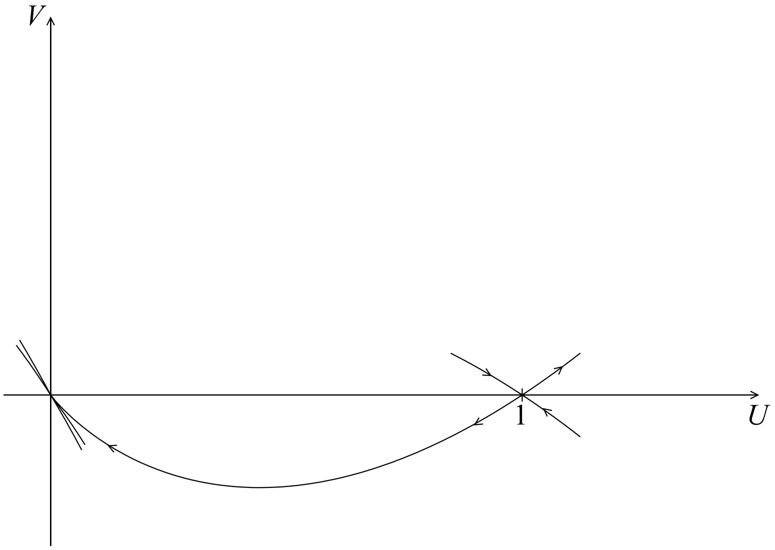

FIGURE 9. Heteroclinic connection from the saddle at $(1,0)$ to the stable node at $(0,0)$. Here $\mu = D = 1$, $c > 2$. There exists a non-negative travelling wave.

mathematically possible as solutions to (13), provided initial conditions are non-negative (Fisher [**7**].)) They correspond to an oscillating front (see Figure 10).

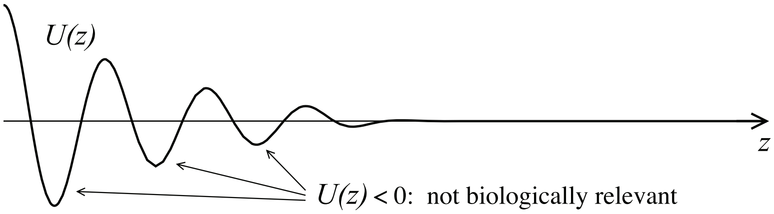

FIGURE 10. Oscillations at the leading edge of the wave from Figure 8.

Hence $c \geq 2$ is a necessary condition for a heteroclinic orbit. Is it a sufficient condition? Because the stable manifold at $P_1 = (0, 0)$ is of dimension 2, it is reasonable to expect that, when $c \geq 2$, a trajectory leaving the saddle at $P_2 = (1, 0)$, as shown in Figure 9, will approach the origin with $U \geq 0$. You are asked to prove this result in the exercise below.

Exercise (Trapping region)

Show that $c \geq 2$ is a sufficient condition for the heteroclinic orbit to exist as shown in Figure 9). A proof can be constructed as follows:

(a) Create a triangular 'trapping region' whose edges are $V = 0$, $U = 1$ and $V = -\alpha U$, $\alpha > 0$.
(b) The unstable manifold at $P_2 = (1, 0)$ emanates out of the equilibrium and into the triangular region. Furthermore, within the triangle, the flow must move to the left. Why?
(c) Start to show that the 'trapping region' is invariant with respect to the flow (the flow starting at any point (U, V) inside the triangle can never leave the triangle). Do this by showing that on the edge $V = 0$, $V' < 0$ and on the edge $U = 1$, $U' < 0$.
(d) Finally show that α can be chosen so that dot product of the inward normal to the line $V = -\alpha U$ and the flow on the line $V = -\alpha U$ is positive. In other words show that α can be chosen so that $(\alpha, 1)\cdot(U, -cU - V(1 - V)) > 0$ whenever $V = -\alpha U$. HINT: show that an α value that satisfies $\alpha^2 - c\alpha + 1 \leq 0$ will do this. Hence a value of α lying between $(c - \sqrt{c^2 - 4})/2$ and $(c + \sqrt{c^2 - 4})/2$ will suffice.
(e) Put the parts of the argument together to conclude that there must be a heteroclinic orbit that stays within the trapping region when $c \geq 2$.

Thus a non-negative travelling wave solution exists for each $c \geq 2$ and no such solution exists for $c < 2$. The minimum wave speed for which there is a positive solution is $c = 2$. In dimensional terms this minimum wave speed is $c = 2\sqrt{rD}$.

The travelling wave problem, expressed in travelling wave coordinates (18) has an alternative 'physical' interpretation if we take U to be displacement of a nonlinear spring and z to be 'time'. Then $U' = V$ is velocity and $V^2/2$ is kinetic energy. We assume that the potential energy in the spring is a nonlinear function of displacement

$$G(U)=\int_0^U g(w)\,dw. \tag{20}$$

Defining the energy to be the sum of kinetic and potential energies $E=V^2/2+G(U)$ we calculate the rate of change of energy as

$$\begin{aligned} E' &= \frac{dE}{dU}U'+\frac{dE}{dV}V' \\ &= g(U)V+V\left(-cV-g(U)\right)=-cV^2. \end{aligned} \tag{21}$$

The last term on the right hand side of the equation can be interpreted as a damping term, with c the friction coefficient. In the case of the Fisher equation, when the spring is stretched close to $U=1$ it moves towards $U=0$. When there is little or no friction the spring will oscillate. The critical wave speed $c=2$ is the critical friction coefficient that prevents oscillation about the well in potential energy that is found at $U=0$. Any friction coefficient that exceeds this value will also prevent oscillations, and will allow the spring to come to rest without overshooting.

Exercise (Energy methods for waves)

Plot $G(U)$ for Fisher's equation and for the bistable equation. Use the above kind of heuristic reasoning to argue that while, Fisher's equation allows travelling waves for all speeds exceeding the minimum speed $c=2$, a heteroclinic connection between $U=1$ and $U=0$ for the bistable equation must have a unique wave speed. (HINT by plotting $G(U)$ show that $U=0$ is not a well in potential energy, but a local peak.)

Although our initial interest was in spread rate of an introduced population, our analysis, so far, has been restricted to travelling waves and their speeds. The relationship between minimum travelling wave speed and spread rate was derived by Aronson and Weinberger [**4**]. Here the spread rate refers to the rate at which a locally introduced population (zero outside a compact set) will spread outwards. Mathematically c^* is the spread rate if, providing the population is introduced locally on a sufficiently large region, a moving reference frame that expands at a speed slower than c^* eventually sees the carrying capacity $u=1$, and a moving reference frame that expands at speed faster than c^* eventually sees the uninvaded steady state. Mathematically these statements are written as for all $0<\epsilon\ll c^*$

$$\lim_{t\to\infty}\ \sup_{|x|>(c^*+\epsilon)t} u(x,t)=0 \tag{22}$$

and

$$\lim_{t\to\infty}\ \sup_{|x|<(c^*-\epsilon)t} |u(x,t)-1|=0 \tag{23}$$

The result from Aronson and Weinberger [**4**] shows that the spread rate for Fisher's equation is exactly the minimum wave speed $c^*=2\sqrt{rD}$.

Returning to the problem of invading a stream system with unidirectional flow, we now include the drift (advection) back into our model (13-14) so that

$$\frac{\partial n}{\partial t}+\frac{\partial}{\partial x}(vn)=D\frac{\partial^2 n}{\partial x^2}+rn\left(1-\frac{n}{K}\right). \tag{24}$$

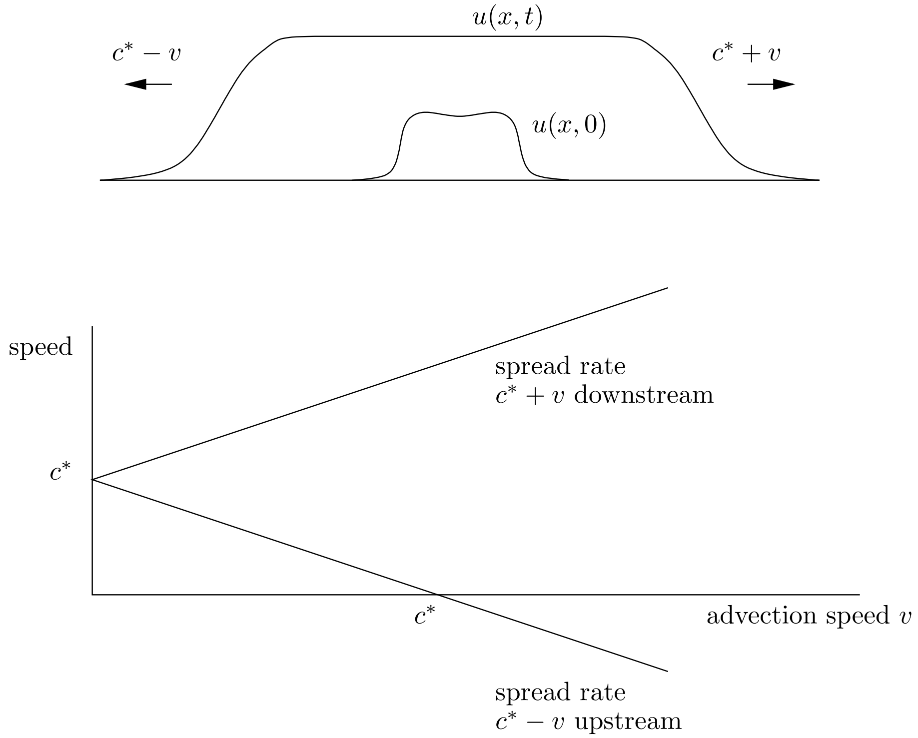

Figure 11. A locally introduced population spreads upstream at rate $c^* - v$ and downstream at rate $c^* + v$. Upstream and downstream spread rates are shown as a function of drift velocity.

However, this drift term is equivalent to simply using a moving reference frame in (13-14). In other words moving from (x, t) to $(x - vt, t)$ transforms (24) to (13-14). Hence, the above analysis can be interpreted as follows. A locally introduced population will spread upstream at speed $c^* - v$ and downstream at speed $c^* + v$. In other words, the population will be successful at spreading upstream when the rate $c^* = 2\sqrt{rD}$ exceeds the drift rate v, and is washed downstream when $v > 2\sqrt{rD}$ (Figure 11).

4. Critical domain size problem

Another measure of whether a population will persist in a stream is whether it will grow when rare. Consider a short stream where the population can grow, outside of which it dies quickly. We start by asking whether the length of stream L is sufficiently large to allow the species to grow when rare. If the length of stream is too small, then individuals will leave the region, move into the hostile surroundings and die. When the stream is long, most individuals can grow and reproduce without leaving the region and moving into the hostile surroundings.

4.1. Classical problem

As we did earlier, we first evaluate the case with zero flow ($v = 0$), and then return to the case $v > 0$ later. As the species is assumed to be rare, it is reasonable to

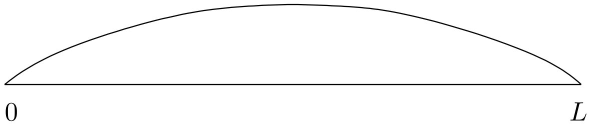

FIGURE 12. A typical solution of (29).

assume that it is at low density. Hence the linearization of (13-14) about $n = 0$ will approximate the dynamics of (13-14). This linearized system, along with boundary conditions indicating a hostile exterior, and an initial condition describing the initial spatial profile of the population is given as

$$\frac{\partial n}{\partial t} = rn + D\frac{\partial^2 n}{\partial x^2}, \quad n(0,t) = n(L,t) = 0, \quad n(x,0) = n_0(x). \tag{25}$$

Because our system is linear, it can be solved by separation of variables. If we consider separable solutions of the form $n \propto \exp(\lambda t)f(x)$, then substitution into (25) yields

$$f'' + \frac{r-\lambda}{D}f = 0, \quad f(0) = f(L) = 0. \tag{26}$$

Solutions $f(x)$ that satisfy the boundary conditions take the form $f(x) = A\cos(\mu x) + B\sin(\mu x)$, where $\mu^2 = (r-\lambda)/D$. The application of boundary condition $f(0) = 0$ implies $A = 0$ and the application of boundary condition $f(L) = 0$ implies $\mu = k\pi/L$. Hence $(k\pi/L)^2 = (r-\lambda)/D$ so $\lambda = r - D(k\pi/L)^2$. Using the principle of superpositioning the solution to (25) is given as

$$n(x,t) = \sum_{k=1}^{\infty} B_k e^{\left(r - D\left(\frac{k\pi}{L}\right)^2\right)t} \sin\left(\frac{k\pi}{L}x\right), \tag{27}$$

where the constants B_k are determined by the initial conditions $n_0(x)$ in equation (25).

Hence the population will grow if $\lambda > 0$ for some k. The fastest growing mode is associated with $k = 1$. In other words, the population will grow if L exceeds

$$L_c = \pi\sqrt{D/r}. \tag{28}$$

Suppose the critical domain size is exceeded and the population grows. How far it will grow? We can answer this question by considering steady state solutions to time-independent version of the nonlinear problem (13-14). Rescaling n by K to yield $u = n/K$, steady state solutions satisfy

$$\frac{r}{D}u(1-u) + u'' = 0, \quad u(0) = u(L) = 0 \tag{29}$$

(Figure 12). Multiplying (29) through by u' and integrating with respect to x yields

$$\frac{w^2}{2} + \frac{r}{D}F(u) = \frac{r}{D}F(\omega), \tag{30}$$

where $F(u) = u^2/2 - u^3/3$ and $w = u'$. This is a Hamiltonian system. In other words it has a first integral (30) that is conserved. Here ω is the maximum value of u which is found at the interior critical point $w = 0$. Symmetry of the diffusion operator and the boundary conditions imply that the maximum occurs at $x = L/2$.

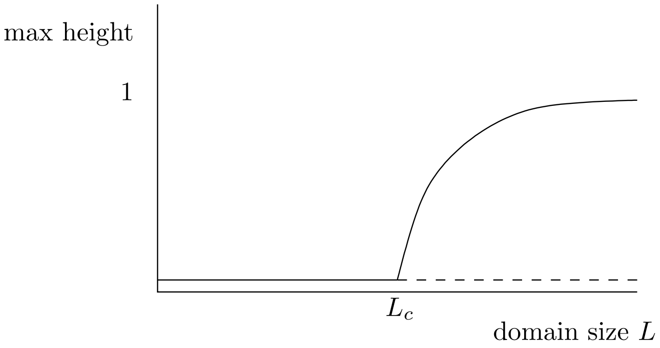

FIGURE 13. A bifurcation curve describing the maximum density of the population μ as a function of the domain size L. Solid lines indicate a stable solution, and dashed lines an unstable.

Hence, on the interval $0 < x < L/2$

$$w = \frac{du}{dx} = \sqrt{\frac{2r}{D}\left(F(\omega) - F(u)\right)}. \tag{31}$$

Separating variables for the previous equation and integrating yields

$$\begin{aligned} L(\omega) &= \sqrt{\frac{2D}{r}} \int_0^{\omega} \frac{du}{\sqrt{(F(\omega) - F(u))}} \\ &= \sqrt{\frac{2D}{r}} \int_0^{1} \frac{\omega dz}{\sqrt{(F(\omega) - F(\omega z))}}, \end{aligned} \tag{32}$$

where $z = u/\omega$. This equation yields a bifurcation diagram for ω versus L. A branch of nontrivial steady state solutions arises from the bifurcation point $(L, \omega) = (\pi\sqrt{D/r}, 0)$ (Figure 13).

Using (32) it is possible to show that, as the maximum value ω approaches zero, L approaches $L_c = \pi\sqrt{D/r}$

Exercise (Bifurcation point in critical domain problem) Using (32), and carefully taking the limit, show that $\lim_{\omega\to 0} L(\omega) = L_c = \pi\sqrt{D/r}$.

4.2. Critical domain size problem in a stream

We now undertake the analysis of the critical domain size problem in the stream ecosystem. Our analysis will conceptually tie together the classical critical domain size problem with travelling wave theory.

When we include drift, the linearized equation (25) becomes

$$\frac{\partial n}{\partial t} + v\frac{\partial n}{\partial x} = rn + D\frac{\partial^2 n}{\partial x^2}, \quad n(0,t) = n(L,t) = 0, \quad n(x,0) = n_0(x). \tag{33}$$

Typical streams have an upstream source, and then empty into a larger body of water. Hence reasonable boundary conditions are zero-flux at the upstream end, where the population cannot leave, and hostile at the downstream end, where environmental conditions may change

$$vn - D\frac{\partial n}{\partial x} = 0 \quad \text{at} \quad x = 0, n = 0 \quad \text{at} \quad x = 0. \tag{34}$$

Proceeding as we did before, the spatial eigenfunction problem becomes

$$\lambda f + vf' = rf + Df'', \quad vf(0) - Df'(0) = 0, \quad f(L) = 0. \tag{35}$$

This kind of problem is referred to as a Sturm-Liouville boundary value problem [**9**]. Solutions that satisfy the boundary conditions take the form

$$f = A\exp(\xi x)\cos(\rho x) + B\exp(\xi x)\sin(\rho x), \tag{36}$$

where $\xi = v/(2D)$ and $\rho = \sqrt{(r-\lambda)/D - (v/(2D))^2}$. Application of the boundary conditions (after some algebra) yields

$$\tan(\rho L) = -2D\rho/v \tag{37}$$

and hence, the critical domain size is given as $\lambda \to 0$ by

$$L = L_c = \frac{\sqrt{D/r}}{\sqrt{1 - v^2/(4rD)}} \arctan\left(-\frac{2\sqrt{rD}}{v}\left(1 - v^2/(4rD)\right)\right). \tag{38}$$

Exercise (Critical stream size problem) Verify equations (36–38). See also the electronic Appendix A of Speirs and Gurney [**15**].

A plot of critical domain size L_c and the up- and down-stream spread rates is given in Figure 14. As the stream velocity reaches the critical speed $c^* = 2\sqrt{rD}$, the critical domain size approaches infinity while the upstream spread rate $c^* - v$ simultaneously approaches zero. That these two events occur simultaneously is intuitively appealing. This also provides a link to two seemingly disjoint areas of analysis in mathematical biology (critical domain size analysis/bifurcation theory for one result and travelling wave/spread rate theory for the other).

Further extensions of this work to include more biological scenarios, such as complex mobile and stationary life-history states (Pachepsky et al [**14**]) and non-diffusive movement via turbulent flow (Lutscher et al [**11**]) have provided a similar connection between the critical domain size and upstream spread rate.

In summary, the mathematical analysis shows that having a positive spread rate is a necessary, but not sufficient condition for persistence when there are hostile downstream boundary conditions. The deleterious effects of these boundary conditions become more pronounced as the stream shortens. These ideas are used in the final section of the Speirs and Gurney paper [**15**], where the authors apply their mathematical results to explaining persistence and extinction in a variety of river ecosystems.

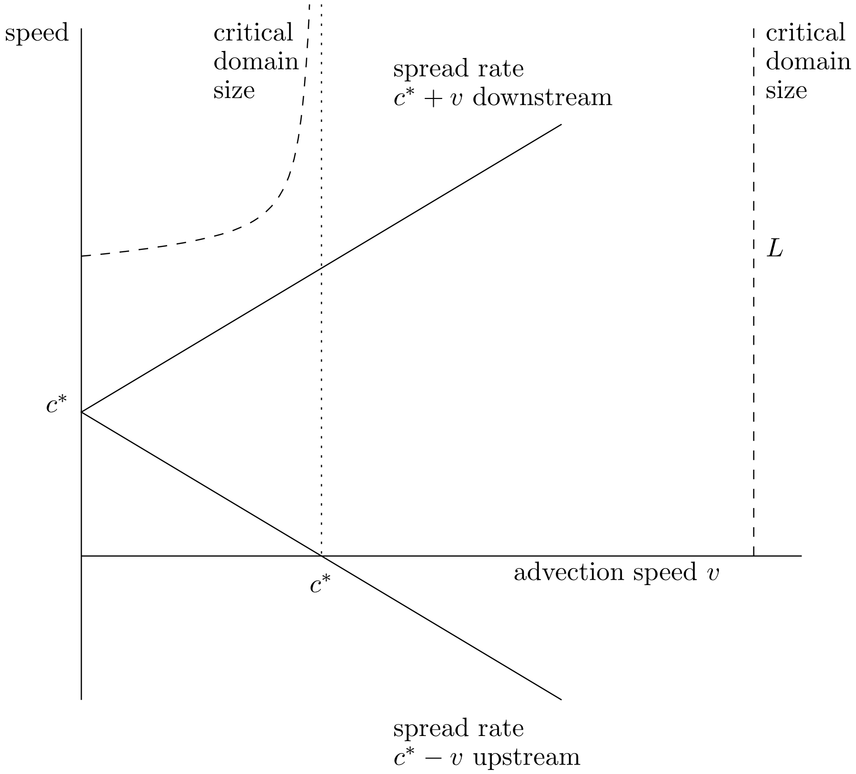

FIGURE 14. A plot of the critical domain size L_c 38 and the up- and down-stream spread rates $c^* - v$ and $c^* + v$ for a range of drift velocities. Note that, for $v = 0$ the critical domain size $\pi\sqrt{D/r}/2$ is exactly half that of the classical problem $\pi\sqrt{D/r}$. This is because of the differing boundary conditions.

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