Diffusion Models of Pattern Formation

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Introduction

The diffusion equation has proven itself to be one of the most significant PDEs (partial differential equations) we have studied. We have used various techniques to solve the diffusion equation in several different situations. Where else can we apply the techniques we have learned? Mathematical ecology is one of the best fields to choose. Solving the diffusion equation in an ecological context provides useful insights and predictions in the context of zoology, botany, and environmental science.

If we wish to study the movement of a certain species, the diffusion equation can show us intriguing patterns. In ecology, the patterns being studied are often two-dimensional. It is useful to think of these patterns as a "bird's-eye view" of the given species. Since our goal is to study patterns of this type, completing a derivation of the two-dimensional diffusion equation is informative. It is also informative to study specific examples of diffusion patterns. In this project, the diffusion patterns of muskrats and insect larvae are analyzed. A brief commentary on reaction-diffusion systems is provided at the end.

Two-Dimensional Diffusion Equation Derivation

Consider the movement of a particle on a two-dimensional plane. At any time, the particle can move a distance of ϵ in any direction. Its displacement is equal to ϵ at times $t, t+\Delta t, t+2\Delta t$, and so on. Since the particle can diffuse in any direction on a two-dimensional plane, we can visualize all possible movement by drawing a circle. Specifically, at time $t+\Delta t$, the particle must lie somewhere on a circle of radius ϵ centered at (x, y), where (x, y) is the position that the particle occupied at time t.

Rather than attempting to determine the position of the particle directly, we use its probability density function (PDF) to speculate where the particle is most likely to land (Pielou, 1969). We could perhaps compare this to electron probability density clouds. In quantum mechanics, the position of an electron in an atom is described by probabilities. The "denser" the cloud is at a certain point, the higher the likelihood that an electron will occupy that space. With this comparison in mind, we denote the PDF of our particle as $\phi(x, y, t+\Delta t)$. At time $t+\Delta t$, the PDF is the mean of $\phi(\xi, \eta, t)$ over all the points (ξ, η) in the circle of radius ϵ centered at (x, y). Recall the mean value theorem for integrals:

$$f(c) = \frac{1}{b-a}\int_a^b f(x)dx.$$

Switch to polar coordinates. The probability density of the particle at time $t+\Delta t$ is

$$\phi(x,y,t+\Delta t) = \frac{1}{2\pi - 0}\int_0^{2\pi} \phi(\xi,\eta,t)d\theta = \frac{1}{2\pi}\int_0^{2\pi} \phi(\xi,\eta,t)d\theta.$$

The stage has been set to derive the two-dimensional diffusion equation. For polar coordinates, we have $x = r\cos\theta$ and $y = r\sin\theta$. To generalize the points in the circle of radius ϵ centered at (x,y), let $\xi = x + \epsilon\cos\theta$ and $\eta = y + \epsilon\sin\theta$. So we have

$$\phi(x,y,t+\Delta t) = \frac{1}{2\pi}\int_0^{2\pi} \phi(x+\epsilon\cos\theta, y+\epsilon\sin\theta, t)d\theta.$$

Left-hand side: the Taylor expansion for $\phi(x,y,t+\Delta t)$, centered at t, is

$$\phi(x,y,t+\Delta t) \;=\; \phi + \frac{\partial\phi}{\partial t}\Big[(t+\Delta t)-t\Big] + \frac{\partial^2\phi/\partial t^2}{2!}\Big[(t+\Delta t)-t\Big]^2 + ... \;=\; \phi + \frac{\partial\phi}{\partial t}\Delta t + \frac{1}{2}\frac{\partial^2\phi}{\partial t^2}(\Delta t)^2 + ...$$

Right-hand side: the Taylor expansion for the integrand, centered at x and y, is

$$\phi(x+\epsilon\cos\theta, y+\epsilon\sin\theta, t) \;=\; \phi + \frac{\partial\phi}{\partial x}\Big[(x+\epsilon\cos\theta)-x\Big] + \frac{\partial\phi}{\partial y}\Big[(y+\epsilon\sin\theta)-y\Big]$$

$$+\frac{\partial^2\phi/\partial x^2}{2!}\Big[(x+\epsilon\cos\theta)-x\Big]^2 + \frac{2\;\partial^2\phi/\partial x\partial y}{2!}\Big[(x+\epsilon\cos\theta)-x\Big]\Big[(y+\epsilon\sin\theta)-y\Big]d\theta + \frac{\partial^2\phi/\partial y^2}{2!}\Big[(y+\epsilon\sin\theta)-y\Big]^2$$

$$= \phi + \frac{\partial\phi}{\partial x}\epsilon\cos\theta + \frac{\partial\phi}{\partial y}\epsilon\sin\theta + \frac{1}{2}\frac{\partial^2\phi}{\partial x^2}(\epsilon\cos\theta)^2 + \frac{\partial^2\phi}{\partial x\partial y}(\epsilon\cos\theta)(\epsilon\sin\theta) + \frac{1}{2}\frac{\partial^2\phi}{\partial y^2}(\epsilon\sin\theta)^2 + ...$$

When we integrate this expression, we obtain

$$\frac{1}{2\pi}\int_0^{2\pi}\Big[\phi + \frac{\partial\phi}{\partial x}\epsilon\cos\theta + \frac{\partial\phi}{\partial y}\epsilon\sin\theta + \frac{1}{2}\frac{\partial^2\phi}{\partial x^2}(\epsilon\cos\theta)^2 + \frac{\partial^2\phi}{\partial x\partial y}(\epsilon\cos\theta)(\epsilon\sin\theta) + \frac{1}{2}\frac{\partial^2\phi}{\partial y^2}(\epsilon\sin\theta)^2 + ...\Big]d\theta$$

$$= \;\frac{1}{2\pi}\int_0^{2\pi}\phi d\theta + \frac{1}{2\pi}\int_0^{2\pi}\frac{\partial\phi}{\partial x}\epsilon\cos\theta d\theta + \frac{1}{2\pi}\int_0^{2\pi}\frac{\partial\phi}{\partial y}\epsilon\sin\theta d\theta$$

$$+\frac{1}{2\pi}\int_0^{2\pi}\frac{1}{2}\frac{\partial^2\phi}{\partial x^2}(\epsilon\cos\theta)^2 d\theta + \frac{1}{2\pi}\int_0^{2\pi}\frac{\partial^2\phi}{\partial x\partial y}(\epsilon\cos\theta)(\epsilon\sin\theta)d\theta + \frac{1}{2\pi}\int_0^{2\pi}\frac{1}{2}\frac{\partial^2\phi}{\partial y^2}(\epsilon\sin\theta)^2 d\theta + ...$$

$$= \;\frac{1}{2\pi}\int_0^{2\pi}\phi d\theta + \frac{\epsilon}{2\pi}\frac{\partial\phi}{\partial x}\int_0^{2\pi}\cos\theta d\theta + \frac{\epsilon}{2\pi}\frac{\partial\phi}{\partial y}\int_0^{2\pi}\sin\theta d\theta$$

$$+\frac{\epsilon^2}{4\pi}\frac{\partial^2\phi}{\partial x^2}\int_0^{2\pi}\cos^2\theta d\theta + \frac{\epsilon^2}{2\pi}\frac{\partial^2\phi}{\partial x\partial y}\int_0^{2\pi}\cos\theta\sin\theta d\theta + \frac{\epsilon^2}{4\pi}\frac{\partial^2\phi}{\partial y^2}\int_0^{2\pi}\sin^2\theta d\theta + ...$$

The first term is exactly how we defined the PDF ϕ (the average over the circle). Other terms simplify as well. We have

$$\int_0^{2\pi} \cos\theta d\theta = \int_0^{2\pi} \sin\theta d\theta = \int_0^{2\pi} \cos\theta \sin\theta d\theta = 0 \qquad \text{and} \qquad \int_0^{2\pi} \cos^2\theta d\theta = \int_0^{2\pi} \sin^2\theta d\theta = \pi.$$

So the right-hand side has simplified to

$$\phi + \frac{\epsilon^2}{4\pi}\frac{\partial^2\phi}{\partial x^2}(\pi) + \frac{\epsilon^2}{4\pi}\frac{\partial^2\phi}{\partial y^2}(\pi) + ... = \phi + \frac{\epsilon^2}{4}\frac{\partial^2\phi}{\partial x^2} + \frac{\epsilon^2}{4}\frac{\partial^2\phi}{\partial y^2} + ... = \phi + \frac{\epsilon^2}{4}\nabla^2\phi + ...$$

where ∇^2 is the two-dimensional Laplacian operator. Compare the left and right sides. We can cancel ϕ. Then we can divide both sides by Δt.

$$\cancel{\phi} + \frac{\partial\phi}{\partial t}\Delta t + \frac{1}{2}\frac{\partial^2\phi}{\partial t^2}(\Delta t)^2 + ... = \cancel{\phi} + \frac{\epsilon^2}{4}\nabla^2\phi + ...$$

$$\frac{\partial\phi}{\partial t} + \frac{1}{2}\frac{\partial^2\phi}{\partial t^2}\Delta t + ... = \frac{\epsilon^2}{4\Delta t}\nabla^2\phi + ...$$

If we take the limit as both Δt and ϵ approach 0, we are left with

$$\frac{\partial\phi}{\partial t} = D\nabla^2\phi$$

where $D = \epsilon^2/4\Delta t$. The two-dimensional diffusion equation has been successfully derived (Pielou, 1969).

Diffusion Pattern 1: Muskrats

In the early 20th century, several concerned parties in Central Europe needed information on the movement of the muskrat *Ondatra zibethicus*. Some hunted the muskrats for fur. Others, such as government officials, had different concerns. "The long list of 'ravages' compiled by Earl De La Warr, parliamentary secretary for the Ministry of Agriculture and Fisheries (MAF), included gnawed crops and (despite being predominantly vegetarian) preying on fish, young poultry, rabbits, and even piglets. The semiaquatic animal's main offense, though, was its inveterate burrowing that undermined the embankments of rivers, canals, ponds, dams, roads, and railways" (Coates, 2020). Skellam (1951) modeled the spread of these muskrats. His results are discussed below.

Revisit the movement of a particle to represent a muskrat. However, this time, rather than considering a single particle, consider a population of particles concentrated at the origin at time $t = 0$. We are interested in the manner in which density falls off with a given distance from the center of diffusion. Let $\Phi(x, y, t)$ denote the proportion of a population to be expected in a certain location at time t. The proportion function resembles the PDF for a Gaussian distribution:

$$\Phi(x, y, t) = \frac{1}{4\pi Dt}\exp\left[\frac{-(x^2 + y^2)}{4Dt}\right].$$

Switching to polar coordinates, we have

$$\Phi(r, \theta, t) = \frac{1}{4\pi Dt}\exp\left(\frac{-r^2}{4Dt}\right).$$

Let $4D = a^2$. Then we have

$$\Phi(r,\theta,t) = \frac{1}{\pi a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right).$$

If we integrate θ out, we obtain the proportion of the population to be expected on the boundary of a circle of radius r. Furthermore, if we integrate r out, we obtain the proportion of the population depending only on time t. We choose our limits of integration as $r = R_t$ to $r = \infty$ where R_t denotes the radius of a circle corresponding to a given contour (see Figure 1). We approximate those contours as circles and proceed to predict how the population will spread in the future.

$$\begin{aligned}
\Phi(t) &= \int_0^{2\pi}\int_{R_t}^{\infty} \frac{1}{\pi a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right) r dr d\theta \int_{R_t}^{\infty}\int_0^{2\pi} \frac{1}{\pi a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right) r d\theta dr \\
&= \int_{R_t}^{\infty}\left[\frac{1}{\pi a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right) r\theta\right]_0^{2\pi} dr = \int_{R_t}^{\infty} \frac{1}{\pi a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right) r(2\pi - 0) dr \\
&= \int_{R_t}^{\infty} \frac{2r}{a^2 t}\exp\left(\frac{-r^2}{a^2 t}\right) dr = \frac{2}{a^2 t}\int_{R_t}^{\infty} r \exp\left(\frac{-r^2}{a^2 t}\right) dr
\end{aligned}$$

$$\text{Let } u = -r^2 \implies du = -2rdr \implies -\frac{1}{2}du = rdr.$$

$$\begin{aligned}
\Phi(t) &= -\frac{1}{a^2 t}\int_*^* \exp\left(\frac{u}{a^2 t}\right) du = -\frac{1}{a^2 t}\left[a^2 t \exp\left(\frac{u}{a^2 t}\right)\right]_*^* \\
&= -\left[\exp\left(\frac{-r^2}{a^2 t}\right)\right]_{R_t}^{\infty} = -\left[\cancelto{0}{\exp(-\infty)} - \exp\left(\frac{-R_t^2}{a^2 t}\right)\right] = \exp\left(\frac{-R_t^2}{a^2 t}\right)
\end{aligned}$$

Denote $\Phi(t)$ as p_t, the proportion of the population expected to be farther than a distance of R_t away from the center of diffusion at time t. Consider a population of size N. If we set $p_t = 1/N$, this equates to choosing a value for p_t (and for R_t) such that exactly one member of the population is expected to be farther than a distance of R_t from the origin. We have

$$p_t = \frac{1}{N} = e^{-R_t^2/a^2 t} \implies e^{R_t^2/a^2 t} = N \implies \ln N = R_t^2/a^2 t \implies R_t^2 = a^2 t \ln N.$$

Consider simple exponential growth for the population: $N_t = N_0 e^{ct}$ where N_t is the population at time t, N_0 is the initial condition, and c is the "intrinsic rate of natural increase" (Pielou, 1969). We have

$$\ln N_t = \ln N_0 e^{ct} \implies \ln N_t = \ln N_0 + \ln e^{ct} \implies \ln N_t = C + ct.$$

Take the constant $C \approx 0$. Then we have

$$R_t^2 = a^2 t \ln N_t \implies R_t^2 = a^2 t(ct) = a^2 c\, t^2.$$

Since the square of the radius is proportional to time squared, we assert that the square root of the area must be approximately proportional to time.

Skellam referenced a contour plot, generated from available data detailing muskrat movement, and approximated each contour as a circle of radius R_t (see Figure 1). This type of movement has been referred to by some as a "pond ripple" pattern:

Figure 1: Contour plot of muskrat movement. Adapted from *Random Dispersal in Theoretical Populations* by J. G. Skellam, 1951, Biometrika, vol. 38, no. 1/2, p. 200. Copyright 1951 by Oxford University Press.

The area within each contour is estimated as πR_t^2. As mentioned earlier, we expect the square root of the area to be proportional to time. Skellam used regression to show that this linear relationship existed (see Figure 2). Any/all concerned parties in need of information on the movement of the muskrats would benefit from the predictions of this model. Using Skellam's approach, we can take given data (contours) and track past and present movement of a given population. We can also predict future movement.

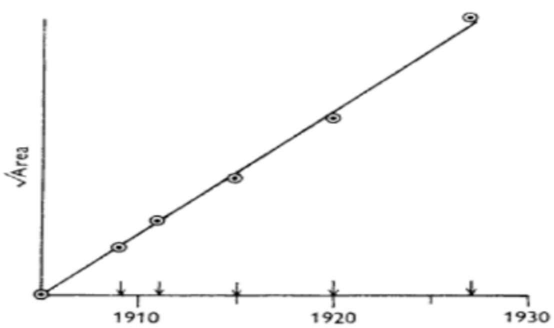

Figure 2: Square root of area covered by muskrats vs. time. Adapted from *Random Dispersal in Theoretical Populations* by J. G. Skellam, 1951, Biometrika, vol. 38, no. 1/2, p. 200. Copyright 1951 by Oxford University Press.

Diffusion Pattern 2: Insect Larvae

Consider an insect laying eggs at the origin of a plane. Upon hatching, the larvae diffuse outward. We can acknowledge the proportion function $\Phi(r, \theta, t)$ again to represent larvae instead of muskrats. Recall that, when we integrated θ out of the double integral, the integrand for the single integral was

$$\Phi(r,t) = \frac{2r}{a^2 t} \exp\left(\frac{-r^2}{a^2 t}\right)$$

where $a^2 = 4D$. This is the proportion of the larvae to be expected on the boundary of a circle of radius r at time t. Multiply both sides by dr for reasons to be seen later:

$$\Phi(r,t)dr = \frac{2r}{a^2t}\exp\left(\frac{-r^2}{a^2t}\right)dr.$$

Assume that, after some movement, a larva stops and remains at the spot it has reached. The travel times for the larvae are independent random variables. Define the associated PDF as $f(t) = \lambda e^{-\lambda t}$ (exponential probability distribution) where $\lambda > 0$.

After all movement has stopped, the distribution of the larvae diffusion is

$$\begin{aligned} g(r)dr =& \left[\int_0^\infty \Phi(r,t)f(t)dt\right]dr \\ =& \left[\int_0^\infty \frac{2r}{a^2t}\exp\left(\frac{-r^2}{a^2t}\right)\lambda\exp(-\lambda t)dt\right]dr \\ =& \left[\int_0^\infty \frac{2r\lambda}{a^2t}\exp\left(-\lambda t - \frac{r^2}{a^2t}\right)dt\right]dr \end{aligned}$$

$$\text{Let } \rho = \frac{2r\sqrt{\lambda}}{a} \implies d\rho = \frac{2\sqrt{\lambda}}{a}dr.$$

$$\begin{aligned} g(r)dr &= \frac{1}{2}\left[\int_0^\infty \frac{2r\sqrt{\lambda}}{a}\exp\left(-\lambda t - \frac{r^2}{a^2t}\right)\frac{dt}{t}\right]\frac{2\sqrt{\lambda}}{a}dr \\ h(\rho)d\rho &= \rho\left[\frac{1}{2}\int_0^\infty \exp\left(-\lambda t - \frac{\rho^2}{4\lambda t}\right)\frac{dt}{t}\right]d\rho \end{aligned}$$

$$\text{Let } \lambda t = \tau \implies dt = \frac{d\tau}{\lambda} \implies dt = \frac{d\tau}{\tau/t} \implies \frac{dt}{t} = \frac{d\tau}{\tau}.$$

$$h(\rho)d\rho = \rho\left[\frac{1}{2}\int_0^\infty \exp\left(-\tau - \frac{\rho^2}{4\tau}\right)\frac{d\tau}{\tau}\right]d\rho$$

If we cancel $d\rho$ on both sides, we are left with $h(\rho) = \rho K_0(\rho)$, where $K_0(\rho)$ is a modified Bessel function of the second kind.

We have studied Bessel functions of the first kind in the context of the drumhead problem. Strauss (2007) provides a summation expression for these functions. Here, the expression for the modified Bessel function of the second kind makes the transition from a discrete to a continuous sum. The DLMF (Digital Library of Mathematical Functions) provides a list of several integral representations for Bessel functions corresponding to different situations. In that list, the relevant integral for our purposes is

$$K_v(z) = \frac{1}{2}\left(\frac{1}{2}z\right)^v\int_0^\infty \exp\left(-t - \frac{z^2}{4t}\right)\frac{dt}{t^{v+1}} \qquad \text{when } \left|\text{ph } z\right| < \frac{\pi}{4}$$

where z is a complex number and ph z is its phase. For insect larvae, ρ plays the role of z where Im $(\rho) = 0$ since ρ must be a real number. If we choose $v = 0$, the integral expressions match and we obtain $K_0(\rho)$.

We have determined that the distribution of insect larvae is $h(\rho) = \rho K_0(\rho)$. The diffusion pattern is radially symmetric. We are interested in the density of the insects at various distances away from the origin, so we plot the number of individuals per unit area (density) vs. distance (see Figure 3). We can see that the modified Bessel function of the second kind only manifests in the first quadrant. This is to be expected since we cannot have a negative number of insects. Modified and unmodified Bessel functions are provided in accompanying slides for visual comparison.

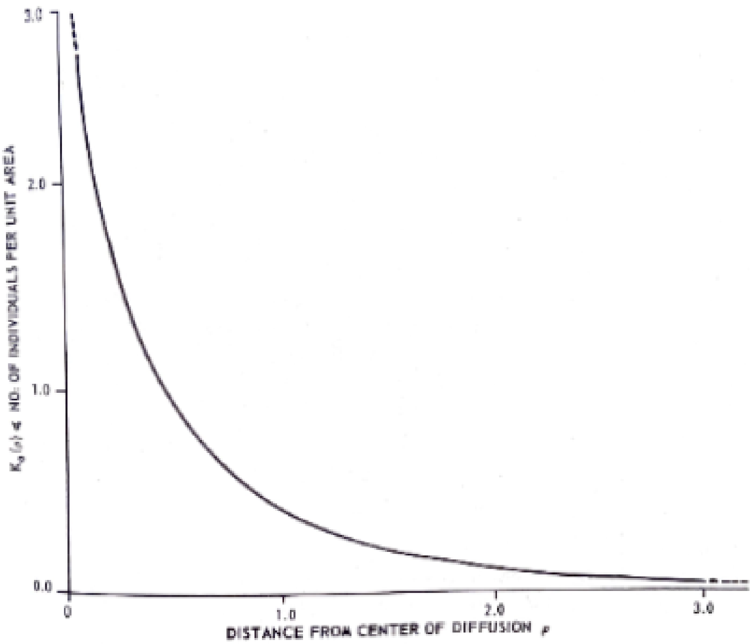

Figure 3: Density of insects vs. distance from hatched eggs. Adapted from *An Introduction to Mathematical Ecology* by E. C. Pielou, 1969, p. 135. Copyright 1969 by John Wiley & Sons, Inc.

Recall the emphasis placed on two-dimensional models in mathematical ecology (see Introduction). At first glance, we might wrongfully speculate that the plot in Figure 3 is modeling diffusion in one spatial dimension. But the plot is indeed modeling a two-dimensional situation. It takes an alternative approach to the "bird's-eye view." The variable ρ involves the radius, so each value for ρ represents a circle. The density of insects is measured on the boundary of each circle. The plot in Figure 3 reveals that the highest densities occur near the origin (where the eggs first hatched). In this example, we can see how random variables, PDFs, and Bessel functions become useful tools in the study of diffusion.

Reaction-Diffusion Systems

Several problems in mathematical ecology are presented as systems of PDEs. Once we gain a firm grasp of a single PDE (e.g. the diffusion equation) and study its applications in ecology, we can make a transition to solving systems that involve that PDE. For example, we can shift our focus to solving reaction-diffusion systems. As the name implies, these systems describe both reactions and diffusion patterns involving at least two different types of particles. In the context of ecology, the "reactions" are usually acknowledged as interactions between two different species.

One dimension. The general form for a reaction-diffusion system can be written as

$$\begin{cases} u_t = D_u u_{xx} + a(u,v) \\ v_t = D_v v_{xx} + b(u,v) \end{cases}$$

where $u(x,t)$ and $v(x,t)$ represent two different types of particles (for example, young and old carbon in a tree root... see slides) and D_u and D_v are the diffusion coefficients for u and v respectively. The functions $a(u,v)$ and $b(u,v)$ are "interaction terms." One common strategy for solving a system of this type is discretization.

In one dimension, we can think of the quantity x as the length measurement of a rod. Break the rod up into compartments of length Δx. In doing so, we "discretize" space. A direct consequence is that the functions u and v depend only on time. So we have $u_i(t) := u(i\Delta x, t)$ and $v_i(t) := v(i\Delta x, t)$ for $i = 1, ..., N$ compartments.

At this point, we should turn our attention to the derivative. The approximation for the second derivative u_{xx} is given as the finite difference

$$u_{xx} \approx \frac{u(x+\Delta x, t) - 2u(x,t) + u(x-\Delta x, t)}{\Delta x^2}$$

with a similar expression for the finite difference approximation for v_{xx}.

For any given compartment, the values for u are affected only by the neighbors immediately to the right or left. The same is true for v. The first PDE becomes the system of ODEs

$$u_i'(t) = \frac{D_u}{\Delta x^2}\Big[u_{i+1}(t) - 2u_i(t) + u_{i-1}(t)\Big] + a(u_i(t), v_i(t))$$

$$i = 2, ..., N-1$$

with similar equations for $v_i'(t)$. So we have two systems of ODEs with a total of $2N$ equations.

For several examples, we wish for energy conservation to apply. In those cases, we should impose Neumann boundary conditions, given as

$$u_x(0,t) = 0, \qquad u_x(L,t) = 0,$$

$$v_x(0,t) = 0, \qquad v_x(L,t) = 0.$$

These are known as reflecting, or sealed-end, boundary conditions (Poll, 2021). Note: these boundary conditions are used for the young/old carbon example. However, old carbon is allowed to leave the system via the surface of the root (see slides). The ODEs for compartments u_1 and u_N on the boundaries are

$$\begin{aligned} u_1'(t) &= \frac{D_u}{\Delta x^2}\Big[u_2(t) - u_1(t)\Big] + a(u_1(t), v_1(t)) \\ u_N'(t) &= \frac{D_u}{\Delta x^2}\Big[u_{N-1}(t) - u_N(t)\Big] + a(u_N(t), v_N(t)) \end{aligned}$$

with similar equations for $v_1'(t)$ and $v_N'(t)$. Organize the compartments for both u and v as vectors. In turn, we can use the second difference matrix S to organize the system:

$$S = \begin{pmatrix} -1 & 1 & 0 & 0 & \cdots & 0 & 0 \\ 1 & -2 & 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & -2 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & 1 & -1 \end{pmatrix} \implies \vec{u}\,' = \frac{D_u}{\Delta x^2} S\vec{u} + a\left(\vec{u}, \vec{v}\right) \quad \text{and} \quad \vec{v}\,' = \frac{D_v}{\Delta x^2} S\vec{v} + b\left(\vec{u}, \vec{v}\right).$$

At this point, the strategy shifts to numerical methods. We can use methods such as the Trapezoidal Rule to approximate the solutions quite accurately. This method is implicit, but in some cases, we can rearrange the equations to obtain an explicit version. If this is possible, the method becomes a simple matter of solving an equation of the form $A\vec{x} = \vec{b}$ at each time step. Results are shown for the young and old carbon in the slides. Those Python plots provide us with much-needed visualizations of the model's predictions of carbon diffusion throughout a one-meter root.

Two dimensions. Consider the following reaction-diffusion system modeling predator-prey dynamics:

$$\begin{cases} u_t = f_u(u) - \alpha v g(u) + D_u \nabla^2 u \\ v_t = \beta v g(u) - f_v(v) + D_v \nabla^2 v \end{cases}$$

where u represents prey density and v represents predator density (Holmes, 1994). The term $f_u(u)$ describes prey population growth in the absence of predators and $-f_v(v)$ describes predator population decline in the absence of prey. As expected, the "interaction term" $-\alpha v g(u)$ predicts prey population decline while $\beta v g(u)$ predicts predator population growth. Lastly, the terms $D_u \nabla^2 u$ and $D_v \nabla^2 v$ describe diffusion of the prey and predators, respectively.

The authors provide two plots of population densities (see Figure 4). These are two possible solutions corresponding to two different sets of parameters and initial conditions. The authors refer to these solutions as the "strips" pattern (left) and the "checkerboard" pattern (right). These patterns can be used to describe the movement of predator/prey populations.

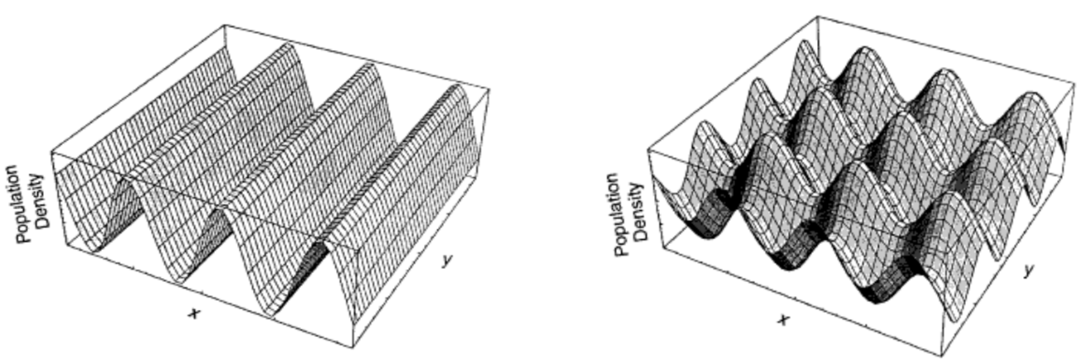

Figure 4: Two possible patterns. Adapted from *Partial Differential Equations in Ecology: Spatial Interactions and Population Dynamics* by E. E. Holmes, 1994, p. 25. Copyright 1994 by the Ecological Society of America.

Moving forward, we need strategies for solving two-dimensional reaction-diffusion systems. The approach outlined for the one-dimensional system (discretization) can be revisited. However, with an additional dimension, the process becomes much more complicated. For the sake of brevity, the one-dimensional process is discussed in greater detail in this project. However, additional examples of two-dimensional predator-prey plots are included in the slides.

Conclusion

The derivation for the diffusion equation gave us a solid foundation on which to move forward with ecological studies. To model the diffusion of a muskrat population, we set up and simplified a PDF. Upon making reasonable assumptions, such as simple exponential growth of the population, we generated a pond ripple pattern. We found that this pattern could be used to describe the movement of the muskrat population. To model the diffusion of insect larvae, we completed rigorous analysis using random variables, PDFs, and Bessel functions. Lastly, we scratched the surface of a challenging task: solving systems of PDEs. Discretization serves as an effective strategy for approximating solutions to reaction-diffusion systems in one or more dimensions.

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