Revisiting the Mathematical Models of Biological Invasions: A Critical Analysis of Shigesada et al. 1995

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Abstract

Modeling Stratified Diffusion in Biological Invasions by Shigesada et al. [1995] proposes three Partial Differential Equation (PDE) systems that model range expansion of invasive species. These models address range expansion by a means of both neighborhood diffusion and long distance migration. The mathematical basis of these models come from the KPP Equation and McKendrick-Von Foerster Equation (MFE). We begin with a summary of the content from Shigesada et al. and highlight ecological insights on the expansion and establishment phases. After discussing how traveling waves play a role in population dynamics, we look into two of Shigesada's models: the short distance dispersal model (SDDM) and the scattered colony model (SCM). We emphasize the ecological assumptions that support these models and discuss the mathematical consequences that these assumptions imply. We deem the SDDM effective at identifying an invasive species's establishment phase and the long term behavior of species that do not expand via long distance migration. On the other hand, the SCM provided valuable short term expansion phase insights for species that expand via stratified diffusion. These results are further mentioned in the discussion where we ponder the validity of Shigesada's approach and propose further research that may be warranted.

1 Introduction

In 1995, Nanako Shigesada and her colleagues contributed to the mathematical modeling of biological invasions with their introduction of several partial differential equation (PDE) based models. Their paper, "Modeling Stratified Diffusion in Biological Invasions," aimed to capture the complex dynamics of invasive species spreading through new environments, focusing particularly on the establishment and expansion phases. These models utilize foundational PDEs, such as Skellam's equation, a derivation of the Kolmogorov-Petrovsky-Piskunov (KPP) equation, and the McKendrick-Von Foerster equation (MFE). As well respected equations in the fields of ecology and population dynamics, these equations offer a structured approach to understanding biological invasions.

The first model from Shigesada et al. [1995], the short distance dispersal model, leverages Skellam's equation to model organisms that disperse primarily through neighborhood diffusion - the notion that organisms spread out locally. The SDDM effectively models less mobile species that cannot migrate long distances and only spread out due to environmental factors such as overcrowding and competition. The second model, the scattered colony model, aims to model stratified diffusion which is when species colonize new areas through both neighborhood diffusion and long distance migration - the act of individuals migrating long distances to establish new "offspring" colonies. Since most organisms experience some form of stratified diffusion, the SCM encapsulates a broader scope of organisms. As we will discuss, however, this model makes a few assumptions that limit its accuracy.

This paper revisits and critically analyzes the the mathematical basis of these two models from Shigesada et al. [1995] We emphasize how the assumptions underlining each model contributes to their ecological and mathematical validity. We rigorously prove the solutions and equations derived in these models, providing a solid mathematical foundation that verifies or challenges their original assertions. This paper proposes alternative mathematical approaches to extrapolate ecological insights. By conducting an independent analysis

of traveling waves within the context of population dynamics, I offer a new perspective on the suitability and limitations of mathematical constructs like the McKendrick-Von Foerster equation in modeling biological invasions.

Lastly, the implications of each model and the ecological insights they provide are thoroughly discussed. For instance, the scattered colony model is shown to offer valid insights only during the early to mid stages of invasion due to issues with the over-calculated area resulting from offspring colony overlap. This critical limitation, along with other model-specific concerns, highlights areas that could benefit from further research and refinement.

By rigorously analysing these models from a mathematical and ecological perspective, this paper not only scrutinizes the work of Shigesada et al. but also offers new areas of concern when studying biological invasions. This paper discusses how contradictions may arise when modeling similar ecological situations using different mathematical approaches.

2 Neighborhood Diffusion: Short Distance Dispersal Model

We consider the Kolmogorov-Petrovsky-Piskunov equation to model the dynamics of an invasive population starting at a point:

$$\begin{cases} \dfrac{\partial n}{\partial t} = D\left(\dfrac{\partial^2 n}{\partial x^2} + \dfrac{\partial^2 n}{\partial y^2}\right) + \epsilon n, \\ n(x, y, 0) = N_0 \delta(x, y), \end{cases} \tag{1}$$

where $D > 0$ and $\epsilon > 0$ are diffusion and growth parameters, respectively. $N_0 > 0$ denotes the size of the initial population and $\delta(x, y)$ is the Dirac delta function. The solution $n(x, y, t)$ describes the population density at a given point (x, y) and time t.

Remark 2.1. *While it is typical for population dynamics models to use the logistic growth term $\epsilon n(1-n/K)$ rather than the exponential growth term when modeling population growth, we do not care about the long term carrying capacity saturation that this term provides. The exponential term is easier to deal with while offering the same insights as logistic growth.*

Proposition 2.2. *Suppose that $n : \mathbb{R}^2 \times \mathbb{R}_+ \to \mathbb{R}$ satisfies the Initial Value Problem (1). Define $N : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}$ by the equality $N(r, t) := n(x^2, \sqrt{r^2 - x^2}, t)$. Then, for all $t > 0$,*

$$N(r, t) = \frac{N_0}{4\pi D t} \exp\left(\epsilon t - \frac{r^2}{4Dt}\right). \tag{2}$$

If this equation does in fact solve (1), then we would note that our solution is in the form of temporally dynamic function that decays exponentially with r. This could inform us of other potential solutions to slightly different models of short distance dispersal.

Proof. Rewrite (1) in terms of r and θ by using the polar Laplacian as outlined in Strauss [2007] (Ch. 6.1): $\Delta n = \frac{\partial^2 n}{\partial r^2} + \frac{1}{r}\frac{\partial n}{\partial r} n + \frac{\partial^2 n}{\partial \theta^2}$. In (1), our diffusion and reaction happens uniformly

in a circular pattern irrespective of θ. Thus, $\frac{\partial^2 n}{\partial \theta^2} = 0$ and (1) become the following:

$$\begin{cases} \dfrac{\partial N}{\partial t} = D\left(\dfrac{\partial^2 N}{\partial r^2} + \dfrac{1}{r}\dfrac{\partial N}{\partial r}\right) + \epsilon N, \\ n(r,0) = N_0\delta(r). \end{cases} \tag{3}$$

Now, to verify the solution, we compute the appropriate derivatives of $N(r,t)$ and plug them into (3). If we are left with a true statement, then (2) solves (3). The appropriate differentials of (2) are as follows:

$$\frac{\partial n}{\partial t} = -\frac{1}{t}N(r,t) + \left(\epsilon + \frac{r^2}{4Dt^2}\right)N(r,t),$$

$$\frac{\partial n}{\partial r} = -\frac{2r}{4Dt}N(r,t) = -\frac{r}{2Dt}N(r,t),$$

$$\frac{\partial^2 n}{\partial r^2} = \frac{\partial n}{\partial r}\left[-\frac{r}{2Dt}N(r,t)\right] = -\frac{1}{2Dt}\left(N(r,t) - \frac{r^2}{2Dt}N(r,t)\right).$$

Now, we rewrite the PDE from (3) and claim:

$$\begin{aligned} &-\frac{1}{t}N(r,t) + \left(\epsilon + \frac{r^2}{4Dt^2}\right)N(r,t) \\ &\qquad = D\left[-\frac{1}{2Dt}\left(N(r,t) - \frac{r^2}{2Dt}N(r,t)\right) - \frac{1}{r}\frac{r}{2Dt}N(r,t)\right] + \epsilon N(r,t). \end{aligned}$$

Let us focus on the right hand side (RHS) and see what it simplifies to. Immediately, we can cancel the constant D in the front, distribute, and combine like terms:

$$\begin{aligned} \text{RHS} &= -\frac{1}{2t}\left(N(r,t) - \frac{r^2}{2Dt}N(r,t)\right) - \frac{1}{2t}N(r,t) + \epsilon N(r,t), \\ &= -\frac{1}{2t}N(r,t) - \frac{1}{2t}N(r,t) + \frac{r^2}{4Dt^2}N(r,t) + \epsilon N(r,t), \\ &= -\frac{1}{t}N(r,t) + \left(\epsilon + \frac{r^2}{4Dt^2}\right)N(r,t) \\ &= \text{LHS}. \end{aligned}$$

Since we have proven the RHS and LHS are equivalent, we can conclude that (2) is a solution to the polar adaptation of our 2D diffusion reaction system. □

Having verified the solution, we must examine how it elucidates the conditions warranting an establishment phase and informs us of the long-term expansion behavior. But, since we verified our solution (2) to Skellam's equation of short distance dispersal, it may worth exploring other models of short distance dispersal. Now, we introduce traveling waves as a potential means of modeling neighborhood diffusion.

3 Qualitative Analysis of Expansion: Traveling Waves

In addition to other more complicated PDEs, certain reaction-diffusion equations have been shown to admit traveling wave solutions [Hou et al., 2023]. One assumption of Shigesada et al. [1995] is that, to some extent, invasive species will spread like a traveling wave. However, it is not straightforward to show that traveling wave solutions exist for the 2D version of our reaction-diffusion equation - Skellam's equation. To demonstrate this, we explore Skellam's equation in 1D without coefficients. After we explore the 1D case, we see that applying a similar argument to the 2D radial Skellam fails. Nevertheless, the authors of Shigesada et al. [1995] continually hint at the presence of traveling waves within this diffusion reaction system. They even propose a custom traveling wave system that is commonly used in population dynamics modeling. This extrapolation, the McKendrick-Von Foerster equation (MFE), will be explored later. Traveling waves are fundamental tools in population dynamics and thus are key in understanding the full scope of this paper.

3.1 TWS to the 1D Skellam Equation

To see how traveling waves emerge from the reaction-diffusion equation, we consider the most basic form of the reaction diffusion equation. This one dimensional reaction diffusion equation contains no constants:

$$\frac{\partial u}{\partial t}(x,t) = \frac{\partial^2 u}{\partial x^2}(x,t) + u(x,t). \tag{4}$$

Notice that in this exercise, we have changed notation to emphasize that this has no physical implication in the context of Shigesada et al. [1995]. The purpose of this 1D traveling wave analysis is to inform how traveling waves are used to solve reaction diffusion systems.

The first step is to suppose that u can be solved with a traveling wave: $u(x,t) = U(x-ct)$. This suggests that our solution can be expressed as a function U that moves to the right at a positive speed c:

$$\frac{\partial U}{\partial t}(x-ct) = \frac{\partial^2 U}{\partial x^2}(x-ct) + U(x-ct). \tag{5}$$

If we let $\xi = x - ct$, then we can transform (5) into an ODE with the following substitutions:

$$\frac{\partial \xi}{\partial t} = -c, \quad \frac{\partial \xi}{\partial x} = 1.$$

By the chain rule, (5) becomes

$$-cU'(\xi) \;=\; U''(\xi) \;+\; U(\xi). \tag{6}$$

Next, we suppose that U is a decaying exponential function. This is a standard assumption with traveling waves. Thus, we make make an ansatz where $U(x-ct) = Ae^{-a\xi}$ for some positive constant a. If we can get a condition for c that makes sense for our system, then the decaying exponential is a solution to (4):

$$\begin{aligned} a^2Ae^{-a\xi} - acAe^{-a\xi} + Ae^{-a\xi} &= 0, \\ a^2 - ac + 1 &= 0, \\ a + \frac{1}{a} &= c. \end{aligned}$$

Here we see that c is positive for all positive a thus, implying that a decaying exponential function solves the 1D Skellam equation.

We can conclude that with appropriate initial conditions, a traveling wave solution with a positive speed exists in the 1D Skellam equation. Analyses like this are how we can justify or reject a traveling wave solution to a reaction diffusion equation.

3.2 TWS With the Radial Skellam Equation

Conducting a similar analysis with the 2D radial version of the Skellam equation presents a conflict. Let us see what (3) becomes when we remove the constants and substitute $N(r,t) = N(r-ct)$ and $\xi = r - ct$ for a wave speed c. Afterward, we have

$$\frac{\partial N(\xi)}{\partial t} = \frac{\partial^2 N(\xi)}{\partial r^2} + \frac{1}{r}\frac{\partial N(\xi)}{\partial r} + N(\xi). \tag{7}$$

Recall that we verified (2) as a solution to Skellam's equation in section 2. Similarly to our 1D Skellam equation traveling wave solution, (2) featured an exponential function. Combining this with what we know about traveling waves makes $N(\xi) = Ae^{-a\xi}$ a valid ansatz to the radial Skellam equation. This guess yields the following substitutions:

$$\begin{aligned}
\frac{\partial N}{\partial t}(\xi) &= cN'(\xi) = -acAe^{-a\xi}, \\
\frac{\partial N}{\partial r}(\xi) &= N'(\xi) = -aAe^{-a\xi}, \\
\frac{\partial^2 N}{\partial r^2}(\xi) &= N''(\xi) = a^2Ae^{-a\xi}.
\end{aligned}$$

With this, we can convert (7) into an ODE and solve just like before:

$$\begin{aligned}
cU'(\xi) &= N''(\xi) + \frac{1}{r}N'(\xi) + N(\xi), \\
-acAe^{-a\xi} &= a^2Ae^{-a\xi} - \frac{1}{r}aAe^{-a\xi} + Ae^{-a\xi}, \\
-ac &= a^2 - \frac{1}{r}a + 1, \\
c &= -a + \frac{1}{r} - \frac{1}{a}.
\end{aligned}$$

When assuming that the decaying exponential solves the radial Skellam equation, we see that the speed of our traveling exponential c is negative and depends on r. This is very hard to avoid considering the radial Laplacian has a factor of $\frac{1}{r}$ in front of the first derivative with respect to r. It is is very difficult to make an ansatz that prevents our speed c from depending on r. Evidently, the TWS of the radial Skellam equation has completely fallen apart. It is possible that there exists a function that satisfies the TWS of the radial Skellam equation, but it is very difficult to achieve analytically.

Even though traveling waves cannot be directly applied to our 2D Skellam equation, Shigesada supposes that they must be somewhere within the short distance dispersal system. Instead of suggesting that population density $N(r,t)$ (the response variable in our Skellam equation) exhibits traveling wave behavior, Shigesada et al. [1995] suggests that the forefront does.

4 The Population Forefront Wave

In hopes of gaining insight on the establishment phase and identifying a traveling wave, we introduce a constant $N^*(r^*, t)$ as a minimum density detection threshold where r^* is the farthest distance from the origin at which a population can be detected. As long as $r^* = 0$, the population is considered to be in its establishment phase. By analysing how r^* changes with t, we reveal the presence of a traveling wave.

4.1 Nondimensionalization

For the sake of ease in dealing with our solution to (3), we nondimensionalize (2) with these substitutions

$$R^* = \sqrt{\frac{\epsilon}{D}} r^*, \qquad T = \epsilon t, \qquad \gamma = \frac{\epsilon N_0}{D N^*}, \tag{8}$$

so that our equation for $R^*(T)$ only depends on an a single constant γ. This allows us to construct a bifurcation diagram and gain insights on the conditions that yield an establishment phase. Using (8), we modify (2) to achieve a nondimensionalized equation for $R^*(T)$:

$$N^* = \frac{N_0 \epsilon}{4\pi D T} \exp\left(T - \frac{r^* \epsilon}{4DT}\right) = \frac{N_0 \epsilon}{4\pi D T} \exp\left(T - \frac{(R^*)^2}{4T}\right).$$

Dividing through by N^* and substituting γ for the constants in the front, we see that

$$1 = \frac{\gamma}{4\pi T} \exp\left(T - \frac{(R^*)^2}{4T}\right).$$

Taking the natural log of both sides and rearranging the RHS gives us:

$$0 = \ln\left(\frac{\gamma}{4\pi T}\right) + T - \frac{(R^*)^2}{4T}$$

Then, we solve for R^* and simplify:

$$R^*(T) \;=\; 2T\sqrt{\frac{1}{T}\ln\frac{\gamma}{4\pi T} + 1} \tag{9}$$

Finally, we have a nondimensionalized equation that outputs the radius R^* of a detectable population for any given input time T.

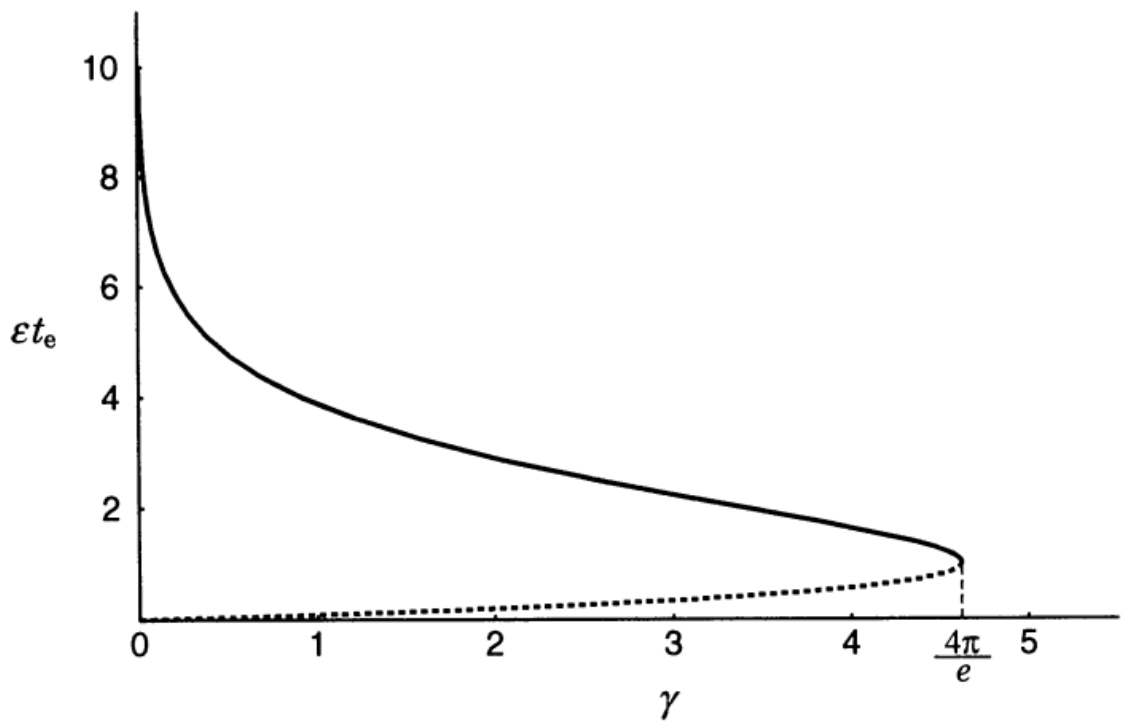
4.2 Establishment Phase

In order to gain insight into the establishment phase, we can alter (9) by setting $R^*(T_e) = 0$ where T_e is the length of an establishment phase. The moment a population has positive R^* is immediately when they exit the establishment phase and enter the expansion phase. By solving for γ, we can find a condition on our establishment phase duration. To do this, we first observe that the $2T$ and square root go away. Then by taking advantage of log properties, we can arrive at

$$\begin{aligned} -1 &= \frac{1}{T_e}\ln\frac{\gamma}{4\pi T_e}, \\ \gamma &= 4\pi T_e e^{-T_e}. \end{aligned} \tag{10}$$

This equation describes the coefficient γ that corresponds to a given establishment phase duration T_e. What we really want, however, is an expression for T_e in terms of γ. Shigesada et al. [1995] achieves this by plotting γ against $T_e = \epsilon t_e$, inverting the graph, and finding the highest γ that yielded a $T_e > 0$:

Figure 1: Bifurcation of ϵt_e with respect to γ (*Shigesada et al. Figure 7*)



Recall from (8) that γ is a known constant relating some minimum detection density threshold with the three constants from our original model. When γ is sufficiently small (i.e. $\gamma < \frac{4\pi}{e}$), this graph suggests that there are two T_e which both satisfy (10), however there can only be one establishment phase associated with each γ. Sending γ to 0 unveils the appropriate T_e. Recall that γ small occurs when the diffusivity constant D and detection density threshold N^* are relatively larger than the reproductive rate ϵ and initial population size N_0. Therefore, a small γ would indicate that we have a small population that continues to diffuse at a rate faster than they can reproduce. These ecological implications lead us to assume that γ small would correspond to a larger establishment phase T_e.

4.2.1 Critical Point Analysis

To avoid dependence on visual figures, I argue that we can differentiate γ with respect to T_e and solve for a local critical point of γ. Therefore, anything above or below the critical point has no corresponding establishment length T_e and thus causes the species to skip the establishment phase.

Proposition 4.1.

$$\frac{d\gamma}{dT_e} = 0 \text{ if and only if } T_e = \frac{4\pi}{e}$$

and if we introduce a $\delta > 0$ small and define perturbations such that

$$T_{e^-} = \frac{4\pi}{e} - \delta, \qquad T_{e^+} = \frac{4\pi}{e} + \delta,$$

then,

$$\frac{d\gamma}{dT_e}(T_{e^-}) > 0, \qquad \frac{d\gamma}{dT_e}(T_{e^+}) < 0.$$

This would imply that T_e is a local maximum.

Proof. Differentiate (10) w.r.t. T_e, set $\frac{d\gamma}{dT_e} = 0$ and solve for T_e to find the local critical point of our $\gamma(T_e)$:

$$\begin{aligned} \gamma &= 4\pi T_e e^{-T_e}, \\ \frac{d\gamma}{dT_e} &= 4\pi e^{-T_e} - 4\pi e^{-T_e}, \\ 0 &= 4\pi e^{-T_e}(1 - T_e). \end{aligned}$$

Thus, only when $T_e = 1$ can $\frac{d\gamma}{dT_e} = 0$, making this the only critical point. We can see that when T_e is δ larger than 1, $\frac{d\gamma}{dT_e} < 0$ and when T_e is δ smaller than 1, $\frac{d\gamma}{dT_e} > 0$ which implies that $T_e = 1$ is a local maximum. □

We have shown that an establishment phase only occurs when $\gamma < \frac{4\pi}{e}$, arriving at the same conclusion provided in *Figure 1*.

4.3 Expansion Phase

The expansion phase comes from (9) by sending T to infinity and observing how R^* grows in relation to T. In this section we can see how traveling waves emerge from the short distance dispersal model. First, take the limit of (9) as follows:

$$\begin{aligned} R^*(T) &= 2T\sqrt{\frac{1}{T}\ln\frac{\gamma}{4\pi T} + 1}, \\ \lim_{T\to\infty} R^*(T) &= \lim_{T\to\infty}\left(2T\sqrt{\frac{1}{T}\ln\frac{\gamma}{4\pi T} + 1}\right). \end{aligned}$$

We need to take a closer look at the first term under the square root:

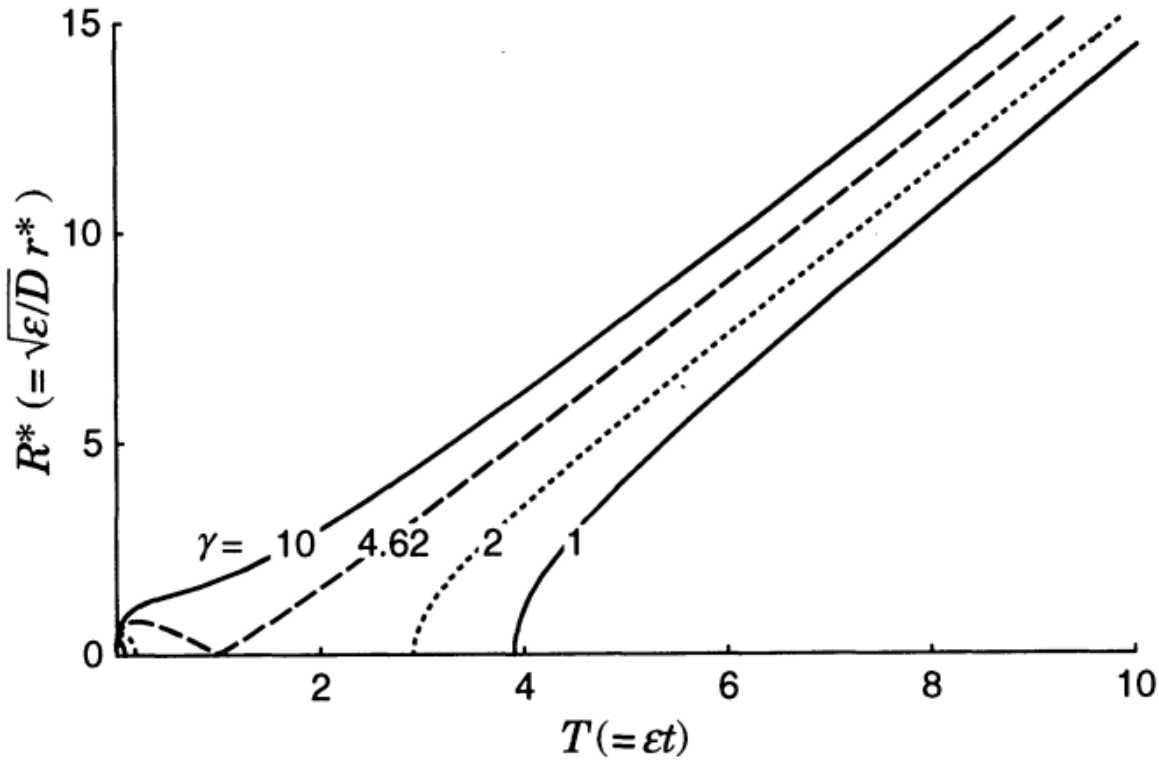
$$\lim_{T\to\infty}\frac{1}{T}\ln\frac{\gamma}{4\pi T} = \lim_{T\to\infty}\frac{1}{T} \times \lim_{T\to\infty}\ln\frac{\gamma}{4\pi T}.$$

Since $\lim_{T\to\infty} \frac{1}{T} \to 0$ faster than $\lim_{T\to\infty} \ln \frac{\gamma}{4\pi T} \to -\infty$, this term zeros out and we can conclude that

$$\lim_{T\to\infty} R^*(T) = \lim_{T\to\infty} 2T. \tag{11}$$

Thus, we know that R^* grows linearly with T by a factor of 2. This takeaway is enforced by Figure 2 from Shigesada et al. [1995] outlining how R^* increases with T for different γ.

Figure 2: Graph of $R^*(T)$ for various γ (*Shigesada et al. Figure 6*)



Notice the long term behavior of the graph tends to slope 2 no matter what γ. When we redimensionalize (11) by substituting R^* and T as defined in (8), we can see how r^* advances in relation to the coefficients from (3):

$$\begin{aligned}
\sqrt{\frac{\epsilon}{D}} r^* &= 2\epsilon t, \\
r^* &= 2\sqrt{\epsilon D} t, \\
\frac{dr^*}{dt} &= 2\sqrt{\epsilon D}.
\end{aligned}$$

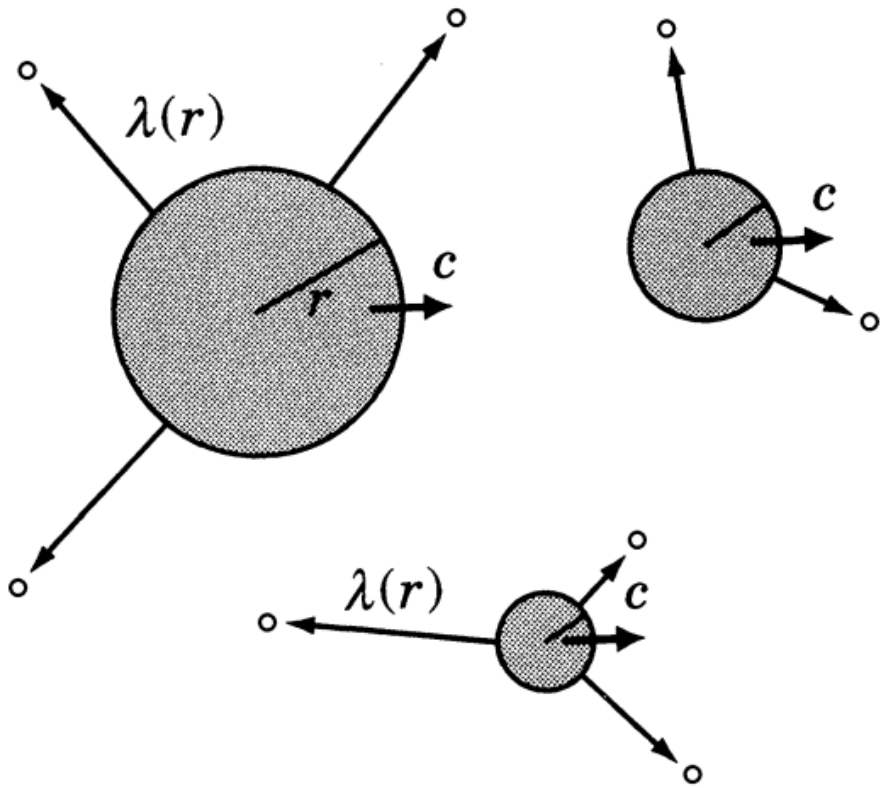
During the expansion phase, we have concluded that the population frontier expands at a rate proportional to twice the square root of their reproductive constant and diffusivity constant. This indicates that populations with high diffusion and growth rates experience rapid range expansion. No matter the γ, our population frontier eventually travels at a constant speed

similar to a traveling wave. Further insight into this exact traveling wave arises later while exploring the scattered colony model (Figure 4) despite its rejection in section 3.2.

5 Stratified Diffusion: Scattered Colony Model

The scattered colony model is Shigesada's first attempt at modeling stratified diffusion. Recall that modeling stratified diffusion involves modeling range expansion resulting from both neighborhood diffusion and long distance migration (LDM). As simple as it sounds, incorporating LDM into a model with neighborhood diffusion is troublesome and requires many assumptions that impact model efficacy and applicability.

Figure 3: Scattered Colonies (*Shigesada et al. Figure 8*)



Shigesada introduces the McKendrick-Von Foerster equation (MFE) which employs a traveling wave component along with very unique boundary and initial conditions. These initial and boundary conditions help make the MFE a popular equation in the field of population dynamics. The MFE is a sensitive model that has been used to describe the evolution of size distribution in which the age of a colony is taken as size and is synonymous with radius r. When we think of a population's "age" as its size, we can model cases where "newborns" are offspring colonies from long distance migration. These offspring colonies can then contribute to the species's total range.

Before we present the model, we must discuss the assumptions made and how these assumptions can lead to limitations in model applications. Firstly, the model presumes that only the founding population engages in long distance migration. Secondly, the model assumes that long distance migrants venture far enough from the original population such that collisions with the parent population occur only after large periods of time. Finally, the model assumes that migrant colonies cannot overlap with one another. Obviously, these assumptions are made to simplify the model and avoid wasting computation. A consequence of these simplification, however, is that this model provides temporally limited insights and does not completely reflect what occurs in nature.

The traveling wave equation and its initial and boundary conditions are as follows:

$$\begin{cases} \dfrac{\partial \rho(r,t)}{\partial t} + c\dfrac{\partial \rho(r,t)}{\partial r} = 0, \\ \rho(r,0) = \delta(r), \\ c\rho(0,t) = \displaystyle\int_0^\infty \lambda(r)\rho(r,t)\,dr. \end{cases} \tag{12}$$

As aforementioned, the initial and boundary conditions are what define this otherwise basic traveling wave PDE as the McKendrick-Von Foerster equation. Similarly to the initial condition from (1), $\rho(r,0) = \delta(r)$ describes that the founders of a population are concentrated at a point centered at the origin. The boundary condition indicates that the number of new colonies created per unit time (LHS) is the total rate at which long-distance migrants succeed in colonization (RHS). Here we introduce a function $\lambda(r)$ that describes the success rate at which long distance migrants establish new colonies. Since different species migrate by different means, $\lambda(r)$ can take on three forms:

$$\lambda(r) = \lambda_0, \;\; \lambda(r) = \lambda_1 r, \;\; \lambda(r) = \lambda_2 r^2,$$
$$\text{for constants } \lambda_0, \lambda_1, \lambda_2 > 0.$$

The first function suggests that successful long distance migrations occur at a constant rate while the others suppose that success depends on the radius or area of the population's range. In case two, $\lambda_1 r$ implies that a population only succeeds in long distance migration when individuals originate from the edge of their range. The scattered colony model simplifies population range to the area of a circle implying that migrations only occur on its circumference. The third case where $\lambda(r) = \lambda_2 r^2$ suggests that long distance migrations succeed according to the area of a population's range.

After solving (12) for $\rho(r,t)$, we can estimate a population's range as a function of time by assigning

$$A(t) = \int_0^\infty \pi r^2 \rho(r,t)\,dr.$$

Plotting area vs. time for different λ informs how various means of long distance migrations impact range expansion. Now the only question that remains is how to solve this system for $\rho(r,t)$ to then extrapolate area functions.

5.1 Solutions to the Scattered Colony Model

The solutions to the scattered colony model are derived by transforming the PDE from (12) into a system of first order linear ordinary differential equations (ODEs). First, we define two more integrals:

$$N(t) = \int_0^\infty \rho(r,t)\,dr,$$
$$R(t) = \int_0^\infty r\rho(r,t)\,dr.$$

$N(t)$, $R(t)$, and $A(t)$ from before, are the total number, sum of radii, and sum of area of colonies respectively. Notice that each expression is $\rho(r,t)$ multiplied by some factor 1, r, and πr^2 and then integrated with respect to r from 0 to infinity. By following a similar process, we can transform our PDE from (12) into equations expressed with $N(t)$, $R(t)$, and $A(t)$. Introducing a general factor $f(r)$, the process begins with

$$\int_0^\infty f(r)\Big(\frac{\partial \rho}{\partial t} + c\frac{\partial \rho}{\partial r}\Big)\,dr = 0.$$

When $f(r) = 1$, we can move the time derivative out front and cancel the radial derivative with the definite integral as follows:

$$\frac{d}{dt}\int_0^\infty \rho(r,t)\,dr + c\rho(r,t)\Big|_0^\infty = 0.$$

Notice that the first term is simply $\frac{d}{dt}N(t)$. The second term can be simplified when we realize that $\rho(\infty,t) = 0$ for all t. Thus, we are left with

$$\frac{d}{dt}N(t) - c\rho(0,t) = 0. \tag{13}$$

The process for $f(r) = r$ and $f(r) = \pi r^2$ requires an extra step of integrating the second term by parts. For example, $f(r) = r$ yields:

$$\int_0^\infty r\frac{\partial \rho}{\partial t}\,dr + c\int_0^\infty r\frac{\partial \rho}{\partial r}\,dr = 0,$$
$$\frac{d}{dt}\int_0^\infty r\rho(r,t)\,dr + c\left[r\rho(r,t)\Big|_0^\infty - \int_0^\infty \rho(r,t)\,dr\right] = 0.$$

Similarly to before, we can notice that $r\rho(r,t)$ is 0 at both ends of the bound, and the other integrals can be substituted for expressions of $R(t)$ and $N(t)$:

$$\frac{d}{dt}R(t) - cN(t) = 0. \tag{14}$$

Repeating this process with $f(t) = \pi r^2$ provides:

$$\frac{d}{dt}A(t) - 2\pi cR(t) = 0. \tag{15}$$

Observe that $c\rho(r,t)$ from (13) is the boundary condition depending on $\lambda(r)$ and $\rho(r,t)$. When we select various $\lambda(r)$, we can rewrite $c\rho(r,t)$ in terms of $A(t)$, $R(t)$, and $N(t)$. Now, we can create a well defined system of three linear first order ODEs using (13-15):

$$\begin{cases} \frac{d}{dt}A(t) - 2\pi c R(t) = 0, \\ \frac{d}{dt}R(t) - cN(t) = 0, \\ \frac{d}{dt}N(t) - c\rho(0,t) = 0. \end{cases} \tag{16}$$

Solving (16) with the three different $\lambda(r)$ using elementary ODE techniques gives us the following equations:

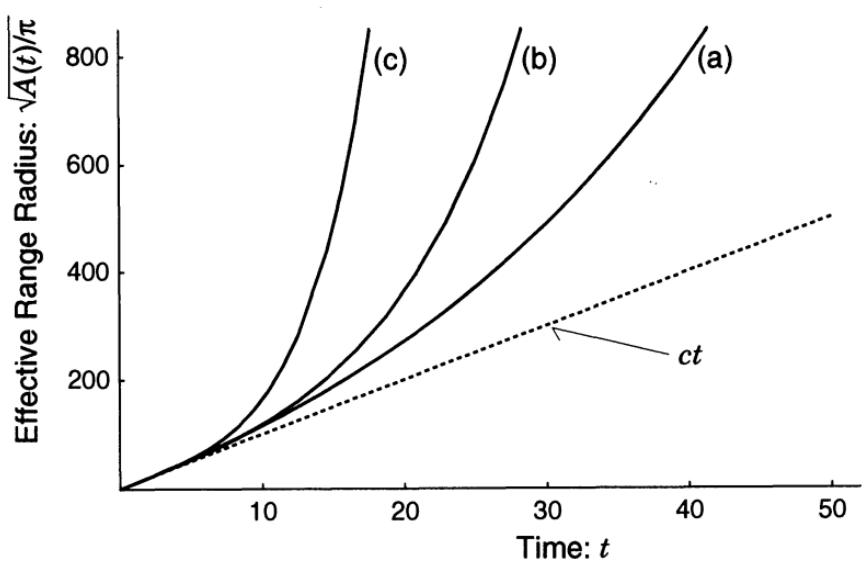
$$\begin{aligned} A(t) &= \frac{2\pi c^2}{\lambda_0}\left(\frac{1}{\lambda_0}(e^{\lambda_0 t} - 1) - t\right), \\ A(t) &= \frac{2\pi c}{\lambda_1} sinh^2\left(\frac{t}{2}\sqrt{c\lambda_1}\right), \\ A(t) &= \frac{2\pi c^2}{3\omega^2}\left(e^{\omega t} + 2e^{\frac{\omega t}{2}} sin\left(\frac{\sqrt{3}}{2}\omega t - \frac{5}{6}\pi\right)\right), \end{aligned} \tag{17}$$

where $\omega = (2c^2\lambda_2)^{\frac{1}{3}}$.

5.2 Model Results and Analysis

Now that we have valid solutions to (12), we can plot the three solutions from (17) for fixed λ_0, λ_1, and λ_2. This figure can provide insight on the benefits of using the scattered colony model while also highlighting fundamental deficiencies.

Figure 4: SCM Range vs. Time for Select $\lambda(r)$ (*Shigesada et al. Figure 9*)



Remark 5.1. *The y axis is the square root of the effective area divided by π. This is so we can see the how the range of our population changes with time instead of how the area changes with time. Transforming our solutions $A(t)$ into units of distance keeps our results and figures consistent with the format from the first section.*

Curves (a), (b), and (c) are the solutions associated with λ_0, $\lambda_1 r$, and $\lambda_2 r^2$ respectively. The dotted curve ct is what our solution looks like when our population does not commit long distance migration (i.e. when $\lambda(r) = 0$). In this case, range expansion only occurs by means of neighborhood diffusion. We will discuss this later.

This model functions under the assumption that LDMs migrate far enough to minimize contact between an offspring colony and the parent population. As such, this model provides good insights for the early to mid expansion phase. If we focus on the area functions where $t < 20$, we can see the implications of all three types of range expansion. During the early to mid expansion phase, LDM populations are isolated. So during this time, (a) is essentially the type 1 linear expansion while (b) is type 2 piece-wise linear and (c) is type 3 exponential. After $t = 20$, however, it appears that offspring colonies begin to encounter the parent population which causes an overlap in area and leads to the species's range to be over calculated. This is an undesired and unavoidable byproduct of the scattered colony model. Since there is no means of accounting for overlapping colonies, there will always exist a time when the scattered colony model begins to over calculate area and thus loses efficacy. While curves (a), (b), and (c) look different, their long-term behaviors all classify them as type three expanders which is known to be false. Even though this defect is inconvenient, the scattered colony model is still effective in modeling early-mid stage range expansion in a wide variety of organisms that undergo stratified diffusion.

Finally, note the dotted line labeled ct. This is the result of setting $\lambda(r) = 0$ and therefore forcing the MFE boundary condition to 0 for all time. Mathematically, when we have this configuration of the MFE, the result is a delta function that moves at a constant speed c. By definition, this is a traveling wave. Ecologically, when we set $\lambda(r) = 0$, we create a model without long distance migration that solely expands via neighborhood diffusion which is just another short distance dispersal model. Quite paradoxically, we see the implication that a traveling wave solution exists to the short distance dispersal model-something we disproved in our radial Skellam traveling wave section. How could this be? We disproved that a decaying exponential-a reasonable guess when discussing population diffusion-can solve the radial Skellam equation. Then, we saw that the solution to the radial Skellam equation converges to a linear expansion rate when we send time to infinity. Clearly there is a disagreement between the MFE and Skellam equation. This brings up suspicions when altering these models and opens up room for new research.

6 Discussion

In this paper, we have examined several PDE systems for modeling types of diffusion in biological invasions. We found that the Skellam equation offers the ability to model neighborhood diffusion, providing key insights into the conditions necessary for an establishment phase and the long-term expansion of populations. Additionally, the McKendrick-Von Foerster equation highlights how offspring colonies contribute to the range of an invasive species,

with long-distance migrations influenced by various spatial properties of the parent colony.

However, our analysis also reveals significant challenges in the structure of these models, particularly when we consider the incorporation of traveling waves in modeling stratified diffusion. These challenges lead us to question the validity of Shigesada's adaptations of the McKendrick-Von Foerster equation (MFE), especially in the Coalescing Colony Model (CCM). This third model proposed by Shigesada attempts to address the interaction where offspring colonies collide and immediately merge with the parent colony—a common ecological event. Unfortunately, the assumptions required by this model, such as the immediate absorption of offspring by the parent colony upon collision, overly simplify complex ecological dynamics and thereby reduce the model's ecological relevance.

Due to these concerns, we have chosen to exclude the CCM from our analysis. We believe that the adjustments required to accommodate these assumptions distort the fundamental equations too significantly, detracting from the model's rigor and application.

Moving forward, exploring the traveling wave solutions to the radial Skellam equation could be particularly insightful. Our paper presents two conflicting results regarding the validity of using traveling waves to model population dynamics. This suggests that a more in-depth examination may yield beneficial findings. Given the complexities associated with the MFE model and its current limitations in handling collision dynamics and various forms of long distance migration rates, we believe that further investigation would enhance these models.

With the advancement of computing technology since Shigesada's original work in 1995, we propose developing a new version of the coalescing colony model that does not rely solely on traveling wave solutions. By directly incorporating features of long-distance migration into the Skellam equation, we could potentially address some of the current shortcomings and provide a more comprehensive model for studying biological invasions. This enhanced approach could accommodate piece-wise or exponential growth rates more effectively, leveraging modern computational resources to offer a more nuanced understanding of invasive species dynamics.

Modeling stratified diffusion is an important achievement in the field of PDE ecology. The models discussed in this paper underscore the lasting value of Shigesada et al. [1995].

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