BIOLOGICAL INVASION IN A PERIODIC ENVIRONMENT

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Abstract. Shigesada *et al.* [8, 10] proposed a reaction-diffusion equation in a periodic environment to model the invasion of biological organisms in heterogeneous environments. However, the model shows a counter intuitive conclusion that a species should decrease its diffusivity in undesirable patches to increase the chance of invasion. Authors show that Fick's diffusion law is the reason for the contradictory phenomenon and that Wereide's diffusion law can fix it. Stability analysis for an invasion condition and the minimum wave speed for a traveling periodic wave are obtained under Wereide's diffusion law. Theoretical results are tested numerically.

1. Introduction

Invasion of a new biological species causes many ecological changes and problems. In a context of population genetics, Fisher [6] proposed a reaction-diffusion equation,

$$u_t = D\Delta u + u(1-u), \tag{1}$$

as a theoretical model to describe spatial invasion of a mutant phenotype. The diffusivity D is constant and the diffusion models a random dispersal in a homogeneous environment. The purpose of the paper is to introduce a heterogeneous diffusion operator to such a biological invasion model in a heterogeneous environment.

Diffusion is a mass transport phenomenon driven by microscopic scale random and chaotic movements which is commonly found in both natural and social phenomena. However, there is no agreement on the correct diffusion equation in a heterogeneous environment when the diffusivity D is nonconstant, i,e., $D = D(\mathbf{x})$. One of most commonly used ones is Fick's law [1],

$$u_t = \nabla \cdot (D(\mathbf{x})\nabla u), \tag{2}$$

where u is the mass density. Remember that a constant state is a steady state solution of (2). Wereide's law [11],

$$u_t = \nabla \cdot (\sqrt{D(\mathbf{x})}\,\nabla(\sqrt{D(\mathbf{x})}\,u)), \tag{3}$$

is also often used. In this case, a constant state is not a steady state anymore. An underlying assumption behind these diffusion laws is that the diffusivity

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alone can decide the diffusion phenomenon even in a heterogeneous environments. On the other hand, a different kind of diffusion law,

$$u_t = \nabla \cdot (\sqrt{\mu^{-1} D}\, \nabla(\sqrt{\mu D}\, u)), \tag{4}$$

has been derived from a revertible velocity jump process, which requires the turning frequency $\mu(\mathbf{x})$ as an extra information. Numerical simulation of the model agrees with a thought experiment and Monte-Carlo simulations (see [7]).

The purpose of the paper is to show that the diffusion law (4) is appropriate in the study of biological invasion in a heterogeneous environment. Having a correct diffusion model is particularly important in the study of biological invasion when the environment is heterogeneous. We will see that inappropriate diffusion models may lead us to wrong conclusions.

Shigesada *et al.* [8, 10] proposed a heterogeneous version of the Fisher-KPP equation (1),

$$u_t = \nabla \cdot (D(x)\nabla u) + (r(x) - u)u, \tag{5}$$

to explain biological invasion phenomenon in a periodically heterogeneous environment. The growth rate r is assumed to be periodic and piecewise constant,

$$r(x) = \begin{cases} 1, & mL < x \le mL + L_a, \\ -r_b, & mL + L_a < x \le mL + L, \end{cases} \tag{6}$$

where $r_b > 0$, $m \in \mathbb{Z}$ integer, and $L_b := L - L_a > 0$. The period is $L > 0$ and the space is divided into favorable patches, $mL < x \le mL + L_a$, with positive growth rate $r = 1$ and unfavorable ones, $mL - L_b < x \le mL$, with negative growth rate $r = -r_b$. The nonconstant diffusivity is piecewise constant and given by

$$D(x) = \begin{cases} 1, & mL < x \le mL + L_a, \\ D_b, & mL + L_a < x \le mL + L, \end{cases} \tag{7}$$

where the diffusivity in the favorable patch is fixed as $D = 1$. An interesting question in this scenario is whether increasing the diffusivity D_b in undesirable patches increases or decreases the chance of invasion. The answer by Shigesada *et al.* from the analysis of (5) is that the survival chance increases if D_b decreases. In other words, a species should decrease its migration in an unfavorable place to increase its survival chance, which is against our common sense (compare the graphs in Figure 1) and a physically wrong conclusion.

The reason for the paradox is in the use of Fick's diffusion law in the SKT model (5). In this paper we take the diffusion law (4). However, since there is no information about the turning frequency in the model of Shigesada *et al.*, we take $\mu = \mu_0$ constant for a neutral comparison. In the case, it actually turns into Wereide's law (3) and gives

$$u_t = \nabla \cdot (\sqrt{D(x)}\nabla(\sqrt{D(x)}u)) + (r(x) - u)u, \tag{8}$$

where r and D are from (6) and (7). This is the model we investigate in the paper. We simply call (5) a "SKT model" and (8) "Our model" in figure legends for brevity. We will see that the invasion chance increases as D_b increases if we take the invasion model (8).

In conclusion, Fick's law (2) is inappropriate in heterogeneous environments and leads to wrong conclusions. On the other hand, the diffusion law (4), or Wereide's law (3) for the case of constant μ, gives physically correct results. Note that there are other components of biological diffusion which are not included in (4). For example, Brownian particles never stop their chaotic movements and the diffusion law in (4) is for such a case. However, biological organisms often have a mechanisms to stay in a favorable place or to leave from an unfavorable one. Such a mechanism should be modeled differently from the diffusivity. The starvation driven diffusion is such a diffusion model which increases the departing probability when starvation started (see [2,3,5]).

2. Weak solution

The existence and the regularity of the solution to the reaction-diffusion equation (5) with Fick's law are understood well when D is bounded. However, the discontinuity in D requires a different care when the solution of (8) is studied.

Definition 2.1. *Let $u:\mathbb{R}\times\mathbb{R}_+\to\mathbb{R}_+$ and $\sqrt{D(x)}u(x,t)$ be $W^{1,1}_{\text{loc}}(\mathbb{R})$ for all fixed $t>0$. We call u a weak solution of (8) if*

$$0=\iint\big(-u\phi_t+\sqrt{D}\,\nabla(\sqrt{D}\,u)\cdot\nabla\phi-(r-u)u\phi\big)dxdt \tag{9}$$

for all test functions $\phi\in C^1_c(\mathbb{R}\times(0,\infty))$.

The diffusivity D is piecewise constant and discontinuous at

$$x_n=\begin{cases} mL, & n=2m,\\ mL+L_a, & n=2m+1,\end{cases} \tag{10}$$

for all $m\in\mathbb{Z}$. The reaction term in (8), $f(x,u)=(r(x)-u)u$, is a smooth function except the discontinuity points x_n in (10). Therefore, the weak solution should satisfy the equation in the classical sense away from the discontinuity points, i.e.,

$$u_t=\begin{cases} u_{xx}+(1-u)u, & mL<x<mL+L_a,\\ D_bu_{xx}-(r_b+u)u, & mL+L_a<x<mL+L.\end{cases} \tag{11}$$

Since the space dimension is one, functions in $W^{1,1}_{\text{loc}}(\mathbb{R})$ are continuous. This gives us the first interface condition at x_n:

$$\lim_{x\to x_n^+}\sqrt{D(x)}u=\lim_{x\to x_n^-}\sqrt{D(x)}u. \tag{12}$$

The second interface condition comes from the continuity of the flux:

$$\lim_{x\to x_n^+}\sqrt{D(x)}(\sqrt{D(x)}u)_x=\lim_{x\to x_n^-}\sqrt{D(x)}(\sqrt{D(x)}u)_x. \tag{13}$$

Theorem 2.2. *Let $u : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}_+$ and $\sqrt{D(x)}u(x,t)$ be $W^{1,1}_{\text{loc}}(\mathbb{R})$ for all fixed $t > 0$. Suppose that u satisfies* (11) *in the classical sense. Then, u satisfies the interface conditions* (12) *and* (13) *if and only if u is a weak solution of* (8).

Proof. Since the space domain is one dimensional, $\sqrt{D(x)}u(x,t)$ is continuous if $\sqrt{D(x)}u(x,t) \in W^{1,1}_{\text{loc}}(\mathbb{R})$ for all fixed $t > 0$. Therefore, we only consider the second interface condition (13).

($\Leftarrow$) Suppose that u is a weak solution. Take a test function $\phi \in C^1_c(\mathbb{R} \times (0,\infty))$ such that $\text{spt}(\phi) \subset (x_{n-1}, x_{n+1}) \times (0,T)$. Let $A = \{(x,t) \in \text{spt}(\phi) : x \le x_n\}$ and $B = \{(x,t) \in \text{spt}(\phi) : x \ge x_n\}$. Then, Eq. (9) gives

$$\iint_{A\cup B} \big(-u\phi_t + \sqrt{D(x)}\,\nabla(\sqrt{D(x)}\,u)\cdot\nabla\phi - (r(x)-u)u\phi\big)dxdt = \iint_A + \iint_B = 0.$$

Since u is a classical solution except the interface $x = x_n$ and the support $\text{spt}(\phi)$ does not touch $t = 0$, after integrating the two by parts, we obtain

$$\iint_A = \int \sqrt{D(x_n^-)}\,\nabla(\sqrt{D(x_n^-)}\,u(x_n^-,t)\phi dt,$$

$$\iint_B = -\int \sqrt{D(x_n^+)}\,\nabla(\sqrt{D(x_n^+)}\,u(x_n^+,t)\phi dt.$$

Therefore,

$$\int \Big(\sqrt{D(x_n^-)}\,\nabla(\sqrt{D(x_n^-)}\,u(x_n^-,t) - \sqrt{D(x_n^+)}\,\nabla(\sqrt{D(x_n^+)}\,u(x_n^+,t)\Big)\phi dt = 0$$

for all test functions $\phi \in C^1_c(\mathbb{R} \times (0,\infty))$ and hence the interface condition (13) is satisfied.

Suppose that the interface condition (13) is satisfied at each interface $x = x_n$. Let $\phi \in C^1_c(\mathbb{R}\times(0,\infty))$ be a test function and $\text{spt}(\phi) \subset (-N,N)\times(0,T)$. Since u satisfies (11) in the classical sense away from the interfaces, we have

$$\begin{aligned}\iint &\big(-u\phi_t + \sqrt{D(x)}\,\nabla(\sqrt{D(x)}\,u)\cdot\nabla\phi - (r(x)-u)u\phi\big)dxdt \\ &= \sum_{n=-N}^{N}\int_0^T \Big(\sqrt{D(x_n^-)}\,\nabla(\sqrt{D(x_n^-)}\,u(x_n^-,t) \\ &\qquad - \sqrt{D(x_n^+)}\,\nabla(\sqrt{D(x_n^+)}\,u(x_n^+,t)\Big)\phi dt \;=\; 0.\end{aligned}$$

Therefore, u is a weak solution. ∎

3. Stability analysis and invasion condition

The model equation (8) has a trivial steady state solution $u = 0$. The stability condition of the trivial solution provides a criterion to decide the ability to invade a new environment. If the trivial solution is stable, a small population size will fail to invade and get extinct eventually. For the analysis, we first linearize the equation (8) at $u = 0$ and obtain

$$v_t = (\sqrt{D(x)}(\sqrt{D(x)}v)_x)_x + r(x)v, \tag{14}$$

where v is considered as a small perturbation of the trivial solution $u = 0$. The corresponding eigenvalue problem is

$$(\sqrt{D(x)}(\sqrt{D(x)}V)_x)_x + (r(x) - \lambda)V = 0, \tag{15}$$

where $V \geq 0$ is a nonnegative eigenfunction corresponding to an eigenvalue λ. Since $D(x)$ and $r(x)$ are piecewise constant, we can explicitly solve (15) piecewise and obtain

$$V(x) = \begin{cases} A_1 \cos\sqrt{1-\lambda}\,(mL + \frac{L_a}{2} - x) \quad + A_2 \sin\sqrt{1-\lambda}\,(mL + \frac{L_a}{2} - x), \\ B_1 \cosh\sqrt{\frac{-1+\lambda}{D_b}}\,(mL - \frac{L_b}{2} - x) + B_2 \sinh\sqrt{\frac{-1+\lambda}{D_b}}\,(mL - \frac{L_b}{2} - x), \end{cases}$$

where $mL < x < mL + L_a$ for the first line and $mL - L_b < x < mL$ for the second one. The environment is symmetric with respect to the mid point of each patch, i.e., with respect to $x = mL + \frac{L_a}{2}$ and $x = mL - \frac{L_b}{2}$. Therefore, the solution V is symmetric with respect to these points. Since $V'(mL + \frac{L_a}{2}) = V'(mL - \frac{L_b}{2}) = 0$, we have $A_2 = B_2 = 0$. If we apply the two interface conditions, (12) and (13), then

$$A_1 \cos\sqrt{1-\lambda}\frac{L_a}{2} = \sqrt{D_b}B_1 \cosh\sqrt{\frac{r_b+\lambda}{D_b}}\frac{L_b}{2},$$

and

$$A_1\sqrt{1-\lambda}\sin\sqrt{1-\lambda}\frac{L_a}{2} = D_b\sqrt{\frac{r_b+\lambda}{D_b}}B_1 \sinh\sqrt{\frac{r_b+\lambda}{D_b}}\frac{L_b}{2}.$$

After dividing the second equation by the first one, we obtain

$$\sqrt{1-\lambda}\tan\sqrt{1-\lambda}\frac{L_a}{2} = \sqrt{r_b+\lambda}\tanh\sqrt{\frac{r_b+\lambda}{D_b}}\frac{L_b}{2}. \tag{16}$$

The λ that satisfies the relation (16) is the principle eigenvalue of the problem (15) since the corresponding eigenfunction V is a singed function. The trivial steady sate $u = 0$ is stable if the principle eigenvalue is negative ($\lambda < 0$) and unstable otherwise (see Nagylaki [9] or Shigesada *et al.* [10]). For a border case $\lambda = 0$, L_a and L_b satisfies,

$$\tan\Big(\frac{L_a}{2}\Big) = \sqrt{r_b}\tanh\Big(\sqrt{\frac{r_b}{D_b}}\frac{L_b}{2}\Big).$$

This relation gives the critical patch size L_b of the unfavorable patches when other parameters are fixed. If the patch size L_b greater than the critical size, i.e.,. if

$$L_b > 2\sqrt{\frac{D_b}{r_b}}\tanh^{-1}\left(\frac{1}{\sqrt{r_b}}\tan\Big(\frac{L_a}{2}\Big)\right),$$

the trivial steady state $u = 0$ becomes stable and invasion of the species fails. Similarly, if the patch size L_b smaller than the critical size, the trivial steady state $u = 0$ becomes unstable and the new species may invade successfully.

Theorem 3.1 (Critical patch size)**.** *For given $L, r, D > 0$, let*

$$F(L, r, D) := 2\sqrt{\frac{D}{r}}\tanh^{-1}\left(\frac{1}{\sqrt{r}}\tan\left(\frac{L}{2}\right)\right). \tag{17}$$

(1) *If $L_b > F(L_a, r_b, D_b)$, $u = 0$ is a stable steady state solution of* (8) *and the invasion fails.*
(2) *If $L_b < F(L_a, r_b, D_b)$, $u = 0$ is an unstable steady state solution of* (8) *and the invasion is successful.*

The corresponding stability analysis for the SKT model (5) is given in [10]. For comparison, we state it in our context;

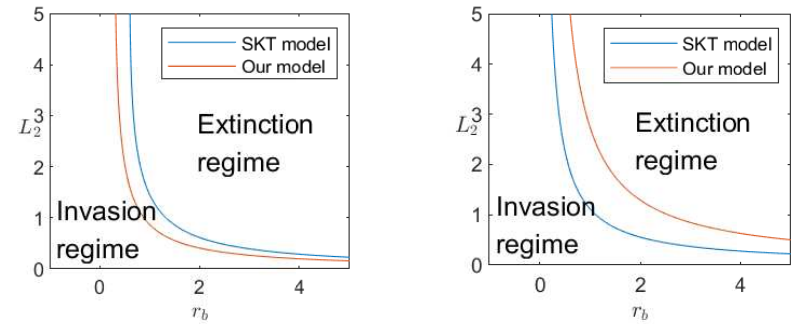
Remark 3.2 (Shigesada *et al.* [10])**.** *Let*

$$\overline{F}(L, r, D) := 2\sqrt{\frac{D}{r}}\tanh^{-1}\left(\frac{1}{\sqrt{rD}}\tan\left(\frac{L}{2}\right)\right). \tag{18}$$

(1) *If $L_b > \overline{F}(L_a, r_b, D_b)$, $u = 0$ is a stable steady state solution of* (5) *and the invasion fails.*
(2) *If $L_b < \overline{F}(L_a, r_b, D_b)$, $u = 0$ is an unstable steady state solution of* (5) *and the invasion is successful.*

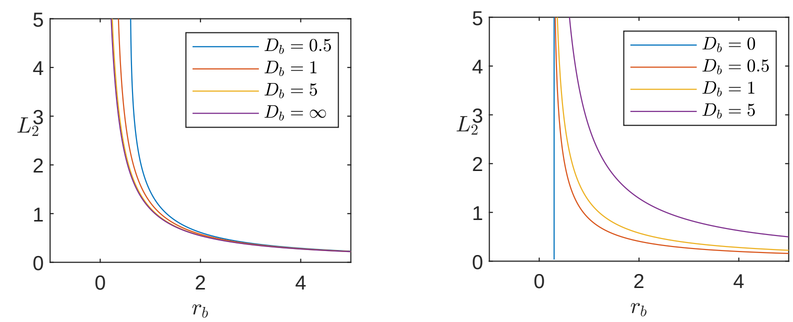
Find a difference and a similarity in the formulas for the critical patch sizes given by (17) and (18). The difference is the coefficient $\frac{1}{\sqrt{rD}}$ inside $\tanh^{-1}$ in the formula for $\overline{F}$. The graphs for the critical interval sizes are given in Figure 1 for the two cases. In the figures, the size of a favorable patches is fixed by $L_a = 1$. Two cases of diffusivity values D_b are considered in the figures. The x-axis in the graph is the negative growth rate r_b in the unfavorable patches. The two models, (5) and (8), are actually identical each other when $D_b = 1$. The parameter regime of SKT model for successful invasion is larger than the one of our model when $D_b < 1$ as given in Figure 1(a). The relation is reversed when $D_b > 1$ as given in Figure 1(b).

The difference of the two models is more clear from Figure 2. The graphs of the critical interval size of the SKT model are given for four cases of diffusivity $D_b = 0.5, 1, 5$, and ∞ in Figure 2(a), where $D_b = \infty$ simply means the asymptotics. We can see that the parameter regime for successful invasion shrinks as D_b increases. This gives a conclusion that a species should reduce its dispersal rate in a unfavorable place to survive. This is a contradictory conclusion and against our common sense. If the environment becomes hostile, a species should move to another place for its survival and hence increasing diffusivity in an unfavorable patch should help its survival. The reason for this contradiction is in Fick's diffusion law which is not a correct diffusion model in a heterogeneous environment.



(a) $D_b = 0.5, L_a = 1$ (b) $D_b = 5, L_a = 1$

FIGURE 1. Graphs for critical patch sizes: x-axis: r_b, y-axis: L_b.



(a) SKT model with Fick's law (b) Our model with Wereide's law

FIGURE 2. Invasion and extinction regimes with $L_a = 1$.

In Figure 2(b), the graphs for critical patch size are given for solutions of our model (8). We can see that the parameter regime for successful invasion expands as D_b increases, which is the opposite result of the SKT model case. This gives an intuitively correct conclusion that a species should increase its dispersal rate in a unfavorable place to increase its chance to invade. Find that the invasion regime is the smallest when $D_b = 0$, i.e., when the species does not move at all in unfavorable patches. In the case, the invasion regime has a vertical boundary. This implies that the size of undesirable patch L_b does not matter if $D_b = 0$. The boundary value r_b is decided by the size of desirable patch L_a.

4. MINIMUM WAVE SPEED

Theorem 3.1 says that, if $L_b < F(L_a, r_b, D_b)$, $u = 0$ is unstable and hence we may expect a traveling periodic wave. In this section, we find the minimum wave speed. To find the wave speed of the reaction-diffusion equation (8), it is enough to consider only the first order term in the reaction function. Hence, we focus in the linearized problem (14) and its solution that satisfies

$$V(x,t) = V(x+L, t+T), \quad x \in \mathbb{R},\ t > 0,$$

where $L > 0$ is the period and $T > 0$. In other words, the solution is a traveling wave type and its speed is given by

$$c = L/T.$$

We will find the minimum traveling wave speed in this section. We are looking for a solution $V(x,t)$ having an asymptotic behavior such that

$$V(x,t) \to 0 \text{ as } x \to \infty \quad \text{and} \quad V(x,t) \to V^*(x) \text{ as } t \to \infty \tag{19}$$

for a wave profile $V^*(x)$. We separate the variables by setting $V = f(z)g(x)$, where $z = x - ct$ is the moving frame variable and $g(x)$ is a periodic function with periodicity L. Substituting $V = fg$ into (14) yields

$$-cf'g = \frac{1}{2}D''fg + \frac{3}{2}D'(f'g + fg') + D(f''g + 2f'g' + fg'') + rfg,$$

where the derivatives of D are considered in a distribution sense at the interfaces $x = x_n$. Divide the equation by f and obtain

$$\frac{f''}{f}Dg + \frac{f'}{f}(cg + \frac{3}{2}D'g + 2Dg') = -\frac{1}{2}D''g - \frac{3}{2}D'g' - Dg'' - rg. \tag{20}$$

Since the right side of (20) is a function of x only, both $\frac{f''}{f}$ and $\frac{f'}{f}$ are constants. We are looking for the asymptotic condition in (19) and set $\frac{f'}{f} = -s$ for some $s > 0$. Then, for a constant $A > 0$, we obtain

$$f = A\exp(-sz).$$

Substituting f into (20) gives

$$\frac{1}{2}D''g + Dg'' + (\frac{3}{2}D' - 2Ds)g' + (r(x) + Ds^2 - cs - \frac{3}{2}D's)g = 0.$$

Since D is a piecewise constant, g satisfies

$$Dg'' - 2Dsg' + (r(x) + Ds^2 - cs)g = 0 \tag{21}$$

in each patch away from the interface, where $r(x) = 1$ in the favorable zone and $r(x) = -r_b$ in the unfavorable one. Solve (21) in $(-L_b, 0)$ and $(0, L_a)$, separately, and obtain

$$g = \begin{cases} e^{sx}(A_1\cosh(q_1x) + A_2\sinh(q_1x)), & 0 < x < L_a, \\ e^{sx}(B_1\cosh(q_2x) + B_2\sinh(q_2x)), & -L_b < x < 0, \end{cases}$$

where

$$q_1 = \sqrt{cs - 1}, \quad \text{and} \quad q_2 = \sqrt{csr_b/D_b}.$$

Remember that q_1 and q_2 depend on c and s.

Next, we apply the interface conditions between two patches, (12)-(13), which are written by

$$\begin{aligned} &\lim_{x\to x_n^+}\sqrt{D(x)}g = \lim_{x\to x_n^-}\sqrt{D(x)}g,\\ &\lim_{x\to x_n^+} D(x)(g'-sg) = \lim_{x\to x_n^-} D(x)(g'-sg). \end{aligned} \tag{22}$$

Since

$$g'(x) = \begin{cases} sg(x) + q_1e^{sx}(A_1\sinh(q_1x) + A_2\cosh(q_1x)), & 0 < x < L_a,\\ sg(x) + q_2e^{sx}(B_1\sinh(q_2x) + B_2\cosh(q_2x)), & -L_b < x < 0, \end{cases}$$

the conditions in (22) give

$$A_1 = \sqrt{D_b}B_1 \quad \text{and} \quad q_1A_2 = D_bq_2B_2. \tag{23}$$

Furthermore, since $g(x) = g(x+L)$, we obtain two more conditions,

$$e^{sL_a}(A_1\cosh(q_1L_a) + A_2\sinh(q_1L_a)) = \sqrt{D_b}e^{-sL_b}(B_1\cosh(q_2L_b) - B_2\sinh(q_2L_b))$$
$$q_1e^{sL_a}(A_1\sinh(q_1L_a) + A_2\cosh(q_1L_a)) = D_bq_2e^{-sL_b}(-B_1\sinh(q_2L_b) + B_2\cosh(q_2L_b)).$$

Substitute (23) and rewrite the system in terms of A_1 and A_2. Then, we obtain

$$\mathbf{M}X = 0,$$

where $X = [A_1, A_2]$ is a column vector and $\mathbf{M} = (M_{ij})$ is a 2×2 matrix given by

$$\begin{aligned} M_{11} &= e^{sL}\cosh(q_1L_a) - \cosh(q_2L_b),\\ M_{12} &= e^{sL}\sinh(q_1L_a) + \frac{q_1}{\sqrt{D_b}q_2}\sinh(q_2L_b),\\ M_{21} &= q_1e^{sL}\sinh(q_1L_a) + q_2\sqrt{D_b}\sinh(q_2L_b),\\ M_{22} &= q_1e^{sL}\cosh(q_1L_a) - q_1\cosh(q_2L_b). \end{aligned}$$

Since $X = [A_1, A_2]$ is a nontrivial solution, the coefficient matrix $\mathbf{M}$ is singular and hence its determinant is zero,

$$0 = \cosh(q_1L_a)\cosh(q_2L_b) + \frac{q_1^2 + D_bq_2^2}{2\sqrt{D_b}q_1q_2}\sinh(q_1L_a)\sinh(q_2L_b) - \cosh(sL). \tag{24}$$

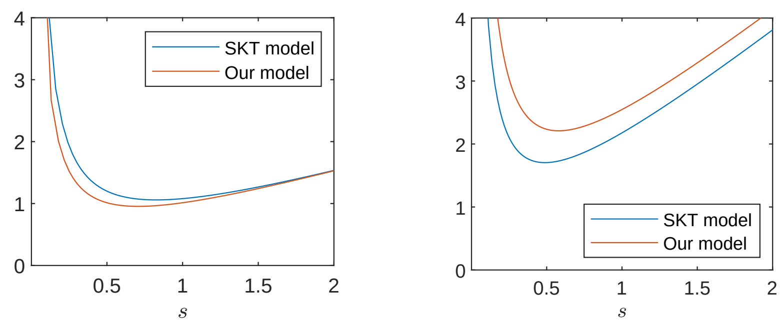
This equality is called the dispersion relation. In this relation, we consider the traveling wave speed $c > 0$ and the parameter $s\ (= f'/f)$ as two variables and others fixed. In other words, we consider c as a function of s, $c = c(s)$, given implicitly by the dispersion relation.

Remark 4.1. *The corresponding dispersion relation for the SKT model* (5) *is given in [10]:*

$$0 = \cosh(q_1L_a)\cosh(q_2L_b) + \frac{q_1^2 + (D_bq_2)^2}{2D_bq_1q_2}\sinh(q_1L_a)\sinh(q_2L_b) - \cosh(sL).$$

The difference is in the quotient part $\frac{q_1^2+(D_b q_2)^2}{2D_b q_1 q_2}$ *and others are identical. If* $D_b = 1$*, the two are identical.*

The graphs of the wave speed c given by the dispersion relation for the SKT model (5) and the model of this paper (8) are given in Figure 3 for two cases. The two curves are supposed to be identical when $D_b = 1$. In the figure, two cases are given with $D_b = 0.5$ and $D_b = 5$. The global minimum points for the four cases are the minimum speeds of the models with the given parameters, which are the observed wave speed.



$r_b = 0.2, D_b = 0.5$ $r_b = 0.2, D_b = 5$

FIGURE 3. Wave speed $c = c(s)$ (x-axis: $s := f'/f$, $L_a = L_b = 1$).

The two model equations of (5) and (8) have the same diffusivity and reaction function. The traveling wave speed is decided by the diffusivity and first order term in Fisher-KPP type reaction diffusion equations in a homogeneous environment. However, the two equations have different minimum speed in heterogeneous environment as observed in Figure 3. Of course, it is already expected when the stability conditions of the trivial solution $u = 0$ are different.

5. Time evolution of solution

In this section, we carry out some numerical simulations to investigate the time evolution of solution to the both models, (5) and (8). We take space domain

$$x \in \Omega := (0.5, 100),$$

with patch sizes,

$$L_a = 1, \quad L_b = 5, \quad \text{and} \quad L = L_a + L_b = 6.$$

The growth rate r and the diffusivity D are given by (6) and (7), respectively. The initial distribution is a Gaussian function given by

$$u_0 = e^{\frac{-(x-0.5)^2}{8}} \quad \text{on} \quad x \geq 0.5,$$

and the boundary condition is by the Neumann boundary condition, i.e.,

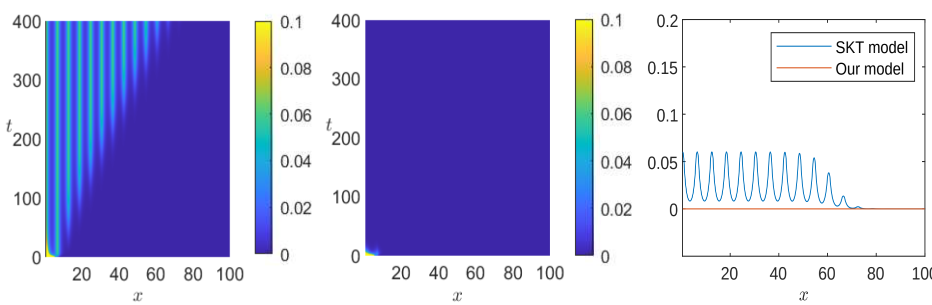
$$u_x(0.5, t) = u_x(100, t) = 0.$$

Find that the spatial heterogeneity in the growth rate r is given by (6). However, the domain boundary is given at $x = 0.5$, not $x = 0$. This is due to the Neumann boundary condition. The space heterogeneity is symmetric with respect to the mid point of each patch and hence the its solution is expected to be symmetric with respect to $x = 0.5$. If one give the Neumann boundary condition at $x = 0$, it will be a case that the size of the first favorable patch is 2 times larger than others.

5.1. **Case 1.** In the first numerical example, we take

$$D_b = 0.5, \quad r_b = 0.5,$$

which belongs to the case that the solution of the SKT model (5) may invade and the solution of the model of this paper (8) get extinct (see Figure 1(a)). For $L_b = 5$, the negative growth rate $r_b = 0.5$ is between the two curves of the figure. Remember that the diffusivity in favorable patch is $D_a = 1$. Hence, it is a case that the species reduces its migration rate in undesirable patches. Intuitively, staying in a harsh place is a wrong behavior.



(a) Time evolution for (5) (b) Time evolution for (8) (c) Solution at $T = 400$

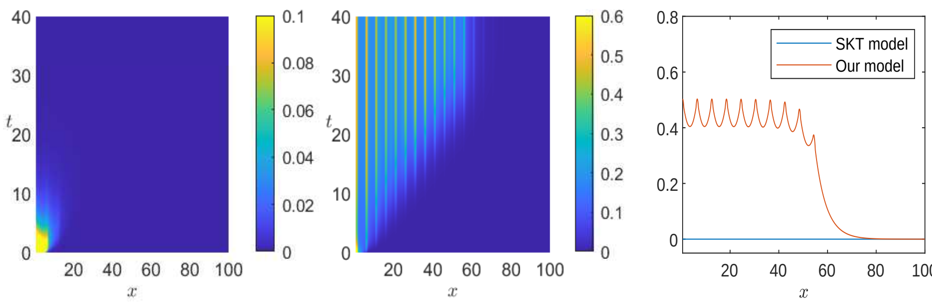
FIGURE 4. Solutions for both models when $D_b = 0.5$ and $r_b = 0.5$

The simulation results are given in Figure 4. We can see that the solution of the SKT model produces oscillating traveling periodic wave and wave speed is approximately $c = 0.19$. However, the solution of the model equation (8) goes extinct. Remember the result of this example and compare the result to the case when species increase migration rate in harsh patches.

5.2. **Case 2.** In the second numerical example, we take

$$D_b = 5, \quad r_b = 0.5,$$

which belongs to the case that the solution of the SKT model (5) goes extinct and the solution of the model of this paper (8) may invade (see Figure 1(b)). For $L_b = 5$, the negative growth rate $r_b = 0.5$ is between the two curves of the figure. In this case, the diffusivity in undesirable patches is $D_b = 5$ which is five times larger than the one in desirable patches. Increasing diffusivity in bad environment is a good strategy to move away from unfavorable places.



(a) Evolution of (5) (b) Evolution of (8) (c) Solution at $T = 40$

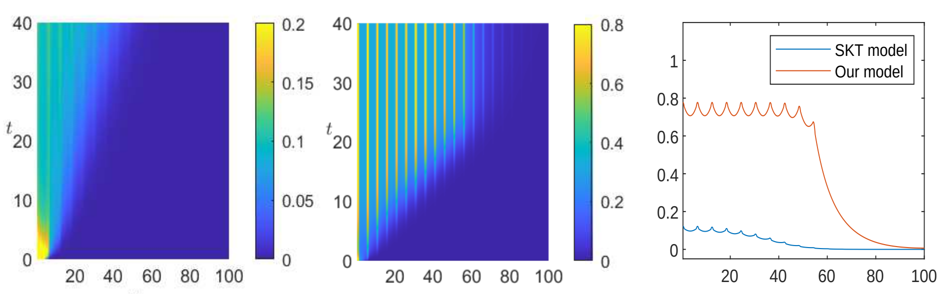
FIGURE 5. Solutions for both models when $D_b = 5$ and $r_b = 0.5$

The simulation results are given in Figure 5. We can see that the solution of the SKT model goes extinct and the solution of the model equation (8) produces oscillating traveling periodic wave and wave speed is approximately $c = 2$. Increasing diffusivity under undesirable environment is a good strategy. However, the solution of SKT model gives opposite result that the species goes extinct and the invasion fails. We should conclude that SKT model (5) does not the model that explains the situation. On the other hand, the solution of the model of the paper (8) gives the correct result that the species starts to survive and the invasion succeeds.

5.3. **Case 3. Both invade.** In the last numerical example, we take

$$D_b = 5, \quad r_b = 0.1,$$

which belongs to the case that the both solutions may invade (see Figure 1(b)). For $L_b = 5$, the negative growth rate $r_b = 0.1$ is placed in the invasion regimes of the two models.



(a) Time evolution of (5) (b) Time evolution of (8) (c) Solution at $T = 40$

FIGURE 6. Solutions for both models when $D_b = 5$ and $r_b = 0.1$

The simulation results are given in Figure 6. We can see that the both solutions produce oscillating traveling periodic wave. The wave speed of SKT model is approximately $c = 1.5$ and the one of our model is approximately $c = 2.5$.

6. Conclusions

In the study of biological invasion in a heterogeneous environment, Fick's diffusion law (2) leads to a physically incorrect conclusion. For example, Shigesada *et al.* [8,10] proposed an invasion model (5) in a periodic environment using Fick's diffusion law. However, the model gives a contradicting result that species should reduce its diffusivity in undesired patches to succeed invasion. The way for a species to avoid undesired patches is to increase the diffusivity and, however, such a behavior harms the species according to the model. It is because Fick's diffusion law does not model dispersal phenomenon correctly in such a heterogeneous environment. The authors derived a diffusion model (4) in a heterogeneous environment using a revertible velocity jump process in [7]. The suggested model (8) in this paper is an application of the diffusion law which fixes the contradictory phenomenon of the SKT model (5). Now, we can say that if the diffusivity is increased in undesired patches, the solution of the new model (8) increases its invasion chance.

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