# On a Finite Population Variation of the Fisher-KPP Equation

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In this paper, we formulate a finite population variation of the Fisher-KPP equation using the fact that the reaction term can be generated from the replicator dynamic using a two-player two-strategy skew-symmetric game. We use prior results from Ablowitz and Zeppetella to show that the resulting system of partial differential equations admits a travelling wave solution, and that there are closed form solutions for this travelling wave. Interestingly, the closed form solution is constructed from a sign-reversal of the known closed form solution of the classic Fisher equation. We also construct a closed form solution approximation for the corresponding equilibrium problem on a finite interval with Dirichlet and Neumann boundary conditions. Two conjectures on these corresponding equilibrium problems are presented and analysed numerically.

#### I. INTRODUCTION

Fisher [1] proposed the following equation

$$\frac{\partial u}{\partial t} = ru(1-u) + \frac{\partial^2 u}{\partial x^2} \tag{1}$$

as a model of the propagation of a mutant genes. At (approximately) the same time, Kolmogorov, Petrovsky and Piskunov analysed a more general version of Eq. (1) [2] with ru(1-u) replaced by a generic function F(u) having prerequisite smoothness and end point properties. Throughout this paper, we refer to Eq. (1) as the Fisher-KPP equation. This equation is known to appear in simple models of susceptible-infected (SI) spatial epidemics with drift [3–5]. It also emerges naturally (often as a simplification) in branching processes [6], for modelling the spread of invasive species [7] and in flame propagation and combustion [8] among other areas.

Solutions (especially travelling wave solutions) to the Fisher-KPP equation have been studied by several authors. Fisher himself studied the existence of wave solutions [1] as did Kolmogorov, Petrovsky and Piskunov [2]. Kametka [9] and Uchiyama [10] studied the asymptotic formation of travelling wave solutions. Later, Newman [11] studied exact solutions. Relevant and related to the brief analysis presented here, Weinberger analysed a discrete form of the Fisher-KPP equation [12]. However, the most relevant result for this work is from Ablowitz and Zeppetella [13] who provide an explicit solution for the Fisher-KPP equation.

The most complete overview of the exact solutions of the Fisher-KPP equation and the more general KPP equation,

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

where f(u) has polynomial form, is available in books of Polynomia et al. [14] and Cherniha et al. [15, 16].

The objective of this paper is to construct a system of partial differential equations modelling both the propagation of a dominant species (allele, infective, competitor etc.) in the presence of a (finite) population experiencing its own spatial evolution. We do so by using a recent formulation by Griffin, Mummah and DeForest for a finite population spatial replicator equation [17]. This work extends earlier work by (among others) Vickers [18] who the studied the spatial replicator with an (assumed) infinite population and work by Durrett and Levin [19] who compared discrete and spatial population dynamics to continuous population dynamics. We show that this system of partial differential equations admits all the travelling wave solutions of the Fisher-KPP equation, except with directions reversed. We use this fact and the results from [13] to derive an explicit example and interpret it in a physical context. We then study the corresponding equilibrium problem for this equation system on a finite interval. We derive a closed form approximation for the Dirichlet problem and use it to construct a conjecture on solution behaviours as the spatial gradient of the population becomes large. A simpler problem with Neumann boundary conditions is also briefly considered.

The remainder of this paper is organized as follows: We derive the model to be studied in Section II. In Section III, we show that travelling wave solutions exist and construct an explicit example. We study the equilibrium problem for

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the equation system in Section IV, constructing a closed form approximation for the problem with Dirichlet boundary conditions as well as two conjectures (to be proven in future work). Conclusions and future directions are presented in Section V.

#### II. MODEL DERIVATION

We begin by deriving the classic Fisher-KPP equation, Eq. (1) as an example of the one-dimensional infinite population spatial replicator equation. Consider a population containing n species. Let  $u_i \in [0,1]$  be the proportion of the total population consisting of species i ( $i \in \{1, ..., n\}$ ). Let  $\mathbf{A} \in \mathbb{R}^{n \times n}$  be an interaction or game matrix so that  $A_{ij}$  encodes the benefit (payoff) to a member of species i from interacting with a member of species j. If  $\mathbf{e}_i$  is the ith standard basis vector in  $\mathbb{R}^n$  and  $\mathbf{u} = \langle u_1, ..., u_n \rangle$ , then the one-dimensional infinite population spatial replicator [18] with diffusion constant k is given by the system of equations,

$$\frac{\partial u_i}{\partial t} = u_i \left( \mathbf{e}_i - \mathbf{u} \right)^T \mathbf{A} \mathbf{u} + k \frac{\partial^2 u_i}{\partial x^2}.$$
 (2)

This equation is composed of a diffusion term added to the standard replicator equation,

$$\dot{u}_i = u_i \left( \mathbf{e}_i - \mathbf{u} \right) \mathbf{A} \mathbf{u}.$$

In the replicator equation, the mean population payoff (fitness) is given by  $\mathbf{u}^T \mathbf{A} \mathbf{u}$  and the proportion  $u_i$  is increasing just in case the expected payoff to species i, given by  $\mathbf{e}_i^T \mathbf{A} \mathbf{u}$ , exceeds the mean population payoff. Let

$$\Delta_{n-1} = \left\{ \mathbf{u} \in \mathbb{R}^n : \sum_i u_i = 1, \ u_i \ge 0 \right\}$$

be the n-1 dimensional unit simplex. The dynamics in Eq. (2) ensure that if the initial conditions place  $\mathbf{u}(0) \in \Delta_{n-1}$ , then the dynamics evolve in  $\Delta_{n-1}$ . The fact that  $\mathbf{u}$  is a vector of population proportions requires such an assumption on the initial condition.

To recover the Fisher-KPP equation, let A be the  $2 \times 2$  skew-symmetric payoff matrix

$$\mathbf{A} = \begin{bmatrix} 0 & -r \\ r & 0 \end{bmatrix}. \tag{3}$$

In this special case,  $\mathbf{u} = \langle u_1, u_2 \rangle$ . With this payoff matrix  $\mathbf{u}^T \mathbf{A} \mathbf{u} = 0$ . Focusing on the equation for  $u_2$ , we can write:

$$\frac{\partial u_2}{\partial t} = ru_2u_1 + k\frac{\partial^2 u_2}{\partial x^2}. (4)$$

Since we started with the spatial replicator, we may assume that  $(u_1, u_2) \in \Delta_1$ , i.e., that  $u_1 + u_2 = 1$ . Therefore, when i = 2, we recover the Fisher-KPP equation,

$$\frac{\partial u_2}{\partial t} = ru_2(1 - u_2) + k \frac{\partial^2 u_2}{\partial r^2},\tag{5}$$

which can simply be written as Eq. (1) with no subscripts and assuming k = 1. The general Fisher-KPP equation does not require  $u \in [0, 1]$ , as would be the case if we view u as a species proportion. However, a straightforward rescaling of u shows that restricting our attention to this interval does not affect the qualitative nature of the solutions.

The dynamics given in Eq. (2) assume a population that is either infinite or spatially homogeneous, or both. Assuming an arbitrary payoff (interaction matrix  $\mathbf{A}$ , for finite populations that are neither infinite nor spatially homogeneous, [17] shows that the spatial replicator in one-dimension becomes the system of equations,

$$\forall i \left\{ \frac{\partial u_i}{\partial t} = u_i \left( \mathbf{e}_i^T \mathbf{A} \mathbf{u} - \mathbf{u}^T \mathbf{A} \mathbf{u} \right) + k \left( \frac{2}{M} \frac{\partial M}{\partial x} \frac{\partial u_i}{\partial x} + \Delta u_i \right) \right.$$

$$\frac{\partial M}{\partial t} = M \mathbf{u}^T \mathbf{A} \mathbf{u} + k \Delta M.$$
(6)

Here, M(x,t) > 0 is the total population of all species at (x,t). As before,  $u_i(x,t)$  is the proportion of the total population composed of species i and consequently  $u_i(x,t)M(x,t)$  is the population of species i at (x,t).

If  $M \to \infty$  and  $\partial_x M$  is bounded or  $\partial_x M = 0$ , and we restrict to one dimension, then this equation is identical to Eq. (2). As with Eq. (2), solutions to Eq. (6) evolve in  $\Delta_{n-1}$  if the initial conditions are in  $\Delta_{n-1}$ .

Using the payoff matrix defined in Eq. (3), we obtain the one dimensional finite population Fisher-KPP system

$$\begin{cases}
\frac{\partial u}{\partial t} = ru(1-u) + \frac{2k}{M} \frac{\partial M}{\partial x} \frac{\partial u}{\partial x} + k \frac{\partial^2 u}{\partial x^2} \\
\frac{\partial M}{\partial t} = k \frac{\partial^2 M}{\partial x^2}.
\end{cases} (7)$$

The population equation is simply a diffusion equation and so (without boundary or initial conditions) we are free to choose any suitable solution. We can use this to find a travelling wave solution to the system of equations, and consequently a closed form solution.

### III. TRAVELLING WAVE SOLUTION

The population (diffusion) equation has a travelling wave solution, given by

$$M(x,t) = A \exp\left[c(x+kct)\right] + B,\tag{8}$$

where A and B are arbitrary constants and  $kc \in \mathbb{R}$  is the wave speed, and  $c \in \mathbb{R}$ . Assume B = 0. Then

$$\frac{1}{M}\frac{\partial M}{\partial x} = c. (9)$$

Let k=1 and let z=x+ct. Following [13], a travelling wave solution for u=u(z) can be found by solving,

$$ru(1-u) + cu' + u'' = 0, (10)$$

with boundary conditions  $\lim_{x\to\infty} u(x) = 0$  and  $\lim_{x\to-\infty} u(x) = 1$ . The travelling wave differential equation for Eq. (1) (the Fisher-KPP equation) is,

$$ru(1-u) - cu' + u'' = 0. (11)$$

This is identical to Eq. (10) except for the sign of the cu' term, which is reversed. Therefore, Eq. (1) and Eq. (7) must share travelling wave solutions but with their directions of travel reversed, assuming the total population is given by Eq. (8).

If we rescale (by letting  $x = \xi/\sqrt{r}$ ), then we obtain an equivalent PDE with r = 1 and we may apply the (astounding) results of Ablowitz and Zeppetella [13] imply, for the special wave speed of:

$$c = \pm \frac{5}{\sqrt{6}},\tag{12}$$

we have the fully closed form solution:

$$u(z) = \left[1 + C \exp\left(\pm \frac{z}{\sqrt{6}}\right)\right]^{-2},\tag{13}$$

where C is another arbitrary constant. We note the solution differs from that in [13] exactly in the sign of z, as a result of the introduction of the finite population term. As we require M(x,t) > 0, it follows that there is only one acceptable solution when c > 0.

Travelling wave solutions u(x,t) and M(x,t) are illustrated in Fig. 1 with  $A=10^{-5}$ , C=1 and  $c=5/\sqrt{6}$ . Plots show snapshots in time with u(x,s) and M(x,s) plotted as functions of x for  $s\in\{0,1,2,3\}$ . The result is biologically interesting because Ablowitz and Zeppetella's construction assumes that  $u(-\infty)=1$  and  $u(\infty)=0$ . We can think of the payoff matrix given in Eq. (3) as describing a prisoner's dilemma game, with strategy (row) two being the dominant one (defect) and strategy (row) one being dominated (cooperate). In this model, u(x,t)=0 corresponds to the presence of only cooperators at position x at time t, while u(x,t)=1 corresponds to the presence of only defectors at position x at time t. Any state with 0 < u(x,t) < 1 corresponds to a mixed population of cooperators and defectors at position x at time t. Such an evolutionary model on a finite lattice is discussed in [20], which references [21] as prior work. Fig. 1 illustrates a solution describing an infinite wave of cooperators who overwhelm the defector population as they move from right to left. This is somewhat contrary to our intuition and to [20], which argues that cooperators survive as small colonies in a "sea of defectors." The phenomena are explained by considering not only the dynamics of u(x,t) but also those of M(x,t). The travelling wave solution on M(x,t) gives an infinite population of cooperators moving from right to left, thus (effectively) swamping the defector population.

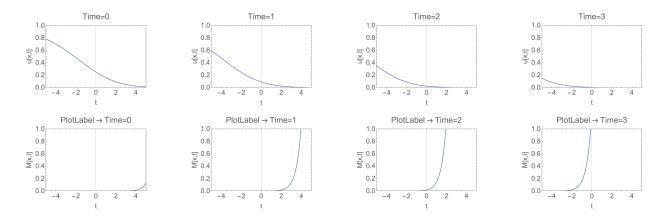


FIG. 1. (Top) Plots of u(x, s) as a function of x for varying values of s. (Bottom) Plots of M(x, s) as a function of x for varying values of s. In these solutions we set  $A = 10^{-5}$ , C = 1,  $c = 5/\sqrt{6}$  and r = k = 1.

#### IV. ASYMPTOTIC BEHAVIOUR IN FINITE REGIONS

#### A. Dirichlet Boundary Conditions

Infinite domain problems are not always relevant to biological or physical problems. Consider the problem

$$\begin{cases}
\frac{\partial u}{\partial t} = ru(1-u) + \frac{2k}{M} \frac{\partial M}{\partial x} \frac{\partial u}{\partial x} + k \frac{\partial^2 u}{\partial x^2} \\
\frac{\partial M}{\partial t} = k \frac{\partial^2 M}{\partial x^2} \\
u(0) = 1 \quad u(1) = 0. \\
M(0) = b \quad M(1) = a + b \\
u(x,0) = u_0(x) \quad M(x,0) = M_0(x).
\end{cases}$$
(14)

We assume b, a + b > 0. The population behaves according to a non-homogeneous heat equation, which has known solution. If we assume the population is at equilibrium so that M(x) = ax + b and consider the equilibrium problem for u(x,t), then the finite population Fisher-KPP equation with Dirichlet boundary conditions becomes,

$$\begin{cases}
\frac{\partial u}{\partial t} = ru(1-u) + \frac{2ak}{ax+b} \frac{\partial u}{\partial x} + k \frac{\partial^2 u}{\partial x^2} \\
u(0) = 1 \quad u(1) = 0. \\
u(x,0) = u_0(x),
\end{cases}$$
(15)

which is the finite analogue of the infinite domain problem. Assume we define

$$u_0(x) = \begin{cases} 1 & \text{if } x = 0\\ 0 & \text{otherwise,} \end{cases}$$

which is consistent with the initial conditions and models a scenario in which a small population of a dominant invasive species is present at the left-boundary of an otherwise uniform population. The fact that M(x) = ax + b with b, a + b > 0 implies that the population size is not homogeneous on this interval. The resulting dynamics for a = 1 and a = 10 and k = r = b = 1 are shown in Fig. 2. The figure illustrates distinct asymptotic behaviour for the two values of a used. For the remainder of this paper, assume k = r = 1. The two-point boundary value problem describing the long-run behaviour is then

$$u'' + \frac{2a}{ax+b}u' + u(1-u) = 0$$

$$u(0) = 1 \quad u(1) = 0,$$
(16)

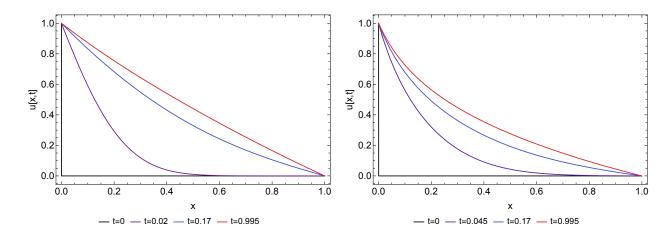


FIG. 2. (Left) Numerical solution for u(x,t) assuming M(x)=1+x. The various curves (in rainbow colours) indicate  $u(x,\tau)$  for varying values of  $\tau$ . (Right) Numerical solution for u(x,t) assuming M(x)=1+10x. The various curves (in rainbow colours) indicate  $u(x,\tau)$  for varying values of  $\tau$ . Both solutions have k=r=1.

where u' indicates differentiation with respect to x. This problem does not appear to be solvable by classical means[22], however the equations arising from linearization at the endpoints are both solvable in closed form. Suppose  $u \approx 1$  and we replace the left-hand boundary condition with boundary conditions u(0) = 1 and  $u'(0) = r_0 < 0$ . The resulting linearized problem

$$u'' + \frac{2a}{ax+b}u' + (1-u) = 0$$
  
 
$$u(0) = 1 \quad u'(0) = r_L.$$

has closed form solution

$$u_L(x; r_L) = \frac{br_L \sinh(x)}{ax + b} + 1.$$

The corresponding right-hand-side problem is given by

$$u'' + \frac{2a}{ax+b}u' + u = 0$$
  
 
$$u(1) = 0 \quad u'(1) = r_R,$$

with solution

$$u_R(x; r_R) = -\frac{r_R(a+b)\sin(1-x)}{ax+b}.$$

As before, we know that  $r_R \leq 0$ . Surprisingly, these solutions can be combined to construct an approximation for the solution of Eq. (16), allowing us to explore the dynamics of the solutions. Let

$$\hat{u}(x;q,r_L,r_R) = \begin{cases} u_L(x;r_L) & \text{if } x \in [0,q) \\ u_R(x;r_R) & \text{if } x \in [q,1]. \end{cases}$$
 (17)

The point q and values for  $r_L$  and  $r_R$  are not known and must be approximated for each input (a, b). We illustrate this in Fig. 3. Assume we are given (a numerical solution for) u(x). From this we can compute  $u'(0) = r_L$  and  $u'(1) = r_R$ . It is easy to compute q by solving the following optimization problem,

$$\arg\min_{q \in [0,1]} \int_0^1 \left[ u(x) - \hat{u}(x;q,r_L,r_R) \right]^2 dx, \tag{18}$$

which can be accomplished using a simple dichotomous or golden section search [23]. Unfortunately, this still requires a numerical solution for u(x) to determine  $r_L$ ,  $r_R$  and q. Our goal in the remainder of this section is to construction

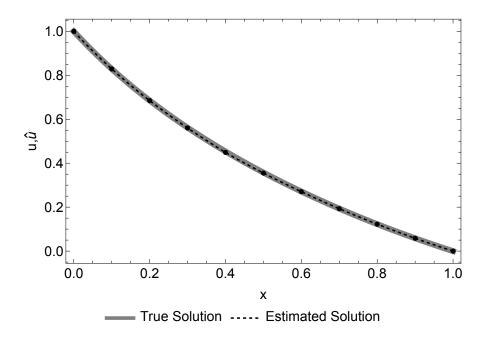


FIG. 3. A comparison of  $\hat{u}$  and u showing goodness of fit of the approximate solution. The computed parameters are q = 0.413,  $r_L = -1.878$  and  $r_R = -0.556$ .

explicit functions that provide these values, thus avoiding the need to repeatedly appeal to a numerical solution. Without loss of generality, we fix b = 1 and show the resulting analysis by varying a only. That is, we will construct closed form representations  $r_L(a)$ ,  $r_R(a)$  and q(a) using a standard ordinary least squares approach. These can then be used in Eq. (17) to build a closed form approximate solution. We use the following procedure to build a data set, on which we will use ordinary least squares regression:

- 1. Choose a from a sample space A with  $a \geq 0$ .
- 2. Compute u(x) using a numerical solver.
- 3. Compute  $r_L = u'(0)$  and  $r_R = u'(1)$  using the output of the numerical solver.
- 4. Compute q using Eq. (18).
- 5. Store  $(a, q, r_L, r_R)$  for fitting.

Following this procedure leads to the data shown in Fig. 4. The data can be fit with the following functions,

$$\hat{q}(a) \sim \frac{1}{(a+\alpha)^{\beta}},\tag{19}$$

$$\hat{r}_L(a) \sim \alpha \cdot a^{\beta}$$
, and (20)

$$r_R(a) \sim \frac{1}{\alpha \cdot a^{\beta}}.$$
 (21)

Tables of fit values are given in the insets of Fig. 4. The adjusted  $r^2$  value for all three fits is  $\sim 0.9999$ , suggesting a high degree of accuracy in the underlying model. Consequently, when b=1 an approximate solution to Eq. (16) is given in closed form by

$$\hat{u}(x;a) \approx \begin{cases} \frac{\sinh(x)\left(-1.03a^{0.996}\right)}{ax+1} + 1 & 0 \le x < \frac{1}{(a+3.29)^{0.621}} \\ -\frac{(a+1)\sin(1-x)\left(-0.883a^{0.993}\right)}{ax+1} & \frac{1}{(a+3.29)^{0.621}} \le x < 1 \end{cases}$$
(22)

Fig. 5 shows anecdotal evidence for the goodness of fit of this approximation for larger values of a. We compute the maximum error

$$E_{\max} = \max_{x} |u(x; a) - \hat{u}(x; a)|$$

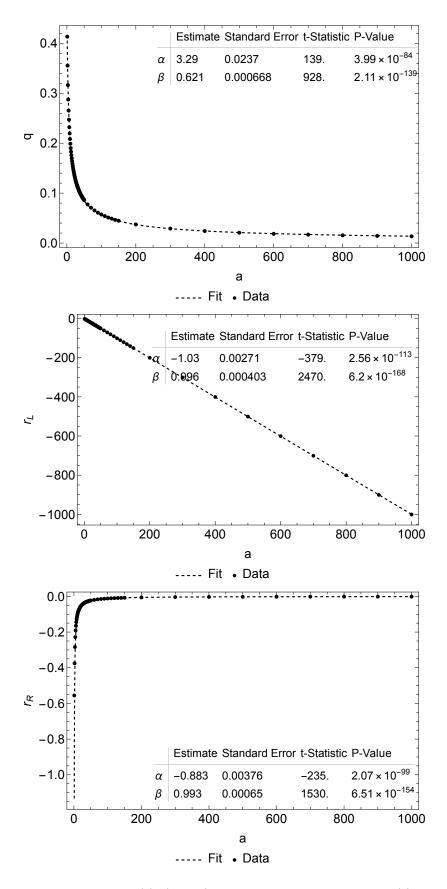


FIG. 4. (Top) Data and corresponding fit for q(a). (Center) Data and corresponding fit for  $r_L(a)$ . Despite the appearance of linearity, there is a slight curvature. (Bottom) Data and corresponding fit for fit of  $r_R(a)$ .

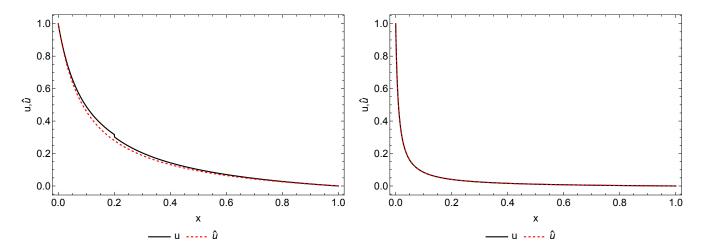


FIG. 5. (Left) The approximation  $\hat{u}$  and u for a=10 shows a reasonable fit with a minor discontinuity. (Right) The approximation  $\hat{u}$  and u for a=100 showing very good fit.

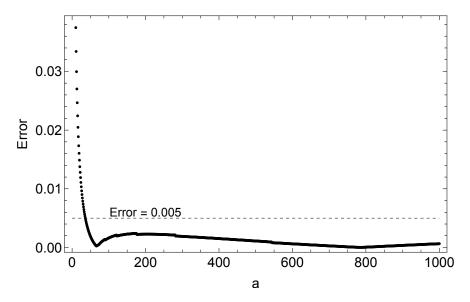


FIG. 6. The maximum error  $E_{\text{max}}$  shows a rapid drop-off as a increases. At a=40, the error is well below 0.005, where it remains.

for  $a \in [0, 1000]$ . This is shown in Fig. 6. The figure shows that for a > 40, the maximum approximation error is well below 0.005, where it remains as a increases. The case of increasing a is interesting because a is (effectively) a measure of how inhomogeneous a population is, assuming that M(0) = b and M(1) = a + b, as given by Eq. (14). In the limit as  $a \to \infty$ , the steady-state ODE becomes

$$u'' + \frac{2}{x}u' + u(1 - u) = 0 \qquad u(0) = 1, \ u(1) = 0,$$

and care must be taken because x = 0 becomes a singular point.

Since Eq. (22) is closed form and the numerical evidence suggests that it is valid for large a, we may use it to extrapolate the following conjecture (to be proved in future work).

**Conjecture 1.** Consider Eq. (16). As  $a \to \infty$ , the solution u approaches the weak solution

$$u(x) = \begin{cases} 1 & \text{if } x = 0 \\ 0 & \text{if } 0 < x \le 1. \end{cases}$$

Interestingly, this behaviour is consistent with the behaviour observed in the travelling wave solution. As  $a \to \infty$ , the population at x = 1 becomes infinite. This is where u(x) = 0. As the system comes to equilibrium, the infinite

population overwhelms the finite population of invaders at x=0, leading to the proposed weak solution. If we reversed the direction of population increase so that (e.g.) M(x)=(a+1)-ax and let  $a\to\infty$ , we would see a limiting population with u(x)=1 for  $0\le x<1$  and u(1)=0.

## B. Neumann Boundary Conditions

It is worth briefly discussing Eq. (16) when the Dirichlet boundary conditions are replaced with Neumann boundary conditions.

$$\begin{cases}
\frac{\partial u}{\partial t} = ru(1-u) + \frac{2ak}{ax+b} \frac{\partial u}{\partial x} + k \frac{\partial^2 u}{\partial x^2} \\
u_x(0) = 0 \quad u_x(1) = 0. \\
u(x,0) = u_0(x),
\end{cases}$$
(23)

The steady state behaviour of this system is relatively easy to predict.

Conjecture 2. Let u(x,t) be a solution to Eq. (23) with  $u_0(x) > 0$  for some x. Then

$$\lim_{t \to \infty} u(x, t) = 1.$$

This conjecture is supported by numerical analysis. Fix  $\epsilon > 0$  and let

$$u_0(x) = \begin{cases} 1 & \text{if } x < \epsilon \\ 0 & \text{otherwise.} \end{cases}$$

This initial condition is consistent with the Neumann boundary conditions. Fig. 7 shows an early transient where u(x,t) drops close to 0 before approaching the constant solution u(x,t) = 1 as the steady state solution.

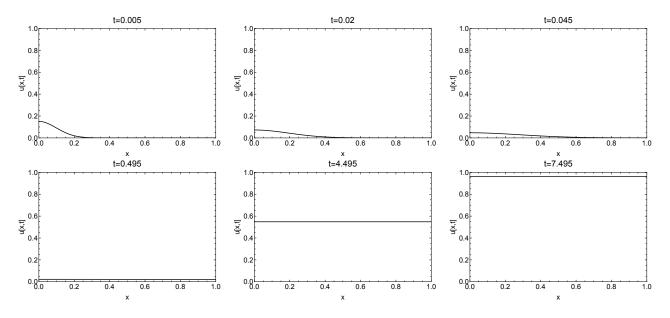


FIG. 7. The time evolution of u(x,t) for t 0.005 to 7.495. The ordering goes left-to-right and top-to-bottom. This supports the conjecture that  $\lim_{t\to\infty} u(x,t)=1$ . Notice, the population homogenizes in space and then approaches u(x,t)=1. Here r=k=a=b=1.

### V. CONCLUSION

In this paper, we studied the finite population Fisher-KPP equation, which arises naturally from the finite population spatial replicator using a skew-symmetric  $2 \times 2$  matrix. We showed using the results of Ablowitz and Zeppetella that

this system of equations admits travelling wave solutions and showed a closed form solution that is identical to that in [13] except that the sign of the wave speed is reversed. We then studied the equilibrium problem for the finite population Fisher-KPP on a finite interval. We constructed a closed form approximate solution to this problem and used it to present a simple conjecture on the behaviour of populations with large spatial gradients.

There are several future directions that could be explored using the proposed finite population Fisher-KPP equation as a basis. For the purpose of this paper, we chose the travelling wave solution to the diffusion equation as the population equation. However, several closed form solutions to the diffusion equation exist and could be used, resulting in a new quasilinear reaction diffusion equation with a convection-like term. Also, in [17] it is noted there are no sensible stable amplitude travelling wave solutions when the logistic term u(1-u) is replaced by a rock-paper-scissors dynamic, which arises from a  $3 \times 3$  skew-symmetric payoff matrices. This paper shows that  $2 \times 2$  skew-symmetric payoff matrices do give rise to travelling wave solutions in the finite population model. Therefore, it would be interesting to know whether any travelling wave solutions exist for  $n \times n$  skew-symmetric payoff matrices with n > 3 or if this is purely a property of  $2 \times 2$  payoff matrices. Proving the conjectures provided in this note are clearly a future direction of work with respect to the finite population Fisher-KPP equation in finite regions. The data-driven analysis method used here could be replaced by a classical perturbation analysis, which might yield even more insight into the behaviour of the solutions. However, an even more interesting direction might be to consider the problem on two-dimensional bounded regions (e.g., disks), where well known solutions to the Laplace equation are available. Studying more exotic boundary conditions (especially in two-dimensions) might also yield interesting results.

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