CRITICAL LENGTH FOR THE SPREADING-VANISHING DICHOTOMY IN HIGHER DIMENSIONS

MATTHEW J. SIMPSON^[D1,*]

(Received 28 February, 2020; accepted 12 April, 2020; first published online 19 June 2020)

Abstract

We consider an extension of the classical Fisher–Kolmogorov equation, called the "Fisher–Stefan" model, which is a moving boundary problem on 0 < x < L(t). A key property of the Fisher–Stefan model is the "spreading–vanishing dichotomy", where solutions with $L(t) > L_c$ will eventually spread as $t \to \infty$, whereas solutions where $L(t) \neq L_c$ will vanish as $t \to \infty$. In one dimension it is well known that the critical length is $L_c = \pi/2$. In this work, we re-formulate the Fisher–Stefan model in higher dimensions and calculate L_c as a function of spatial dimensions in a radially symmetric coordinate system. Our results show how L_c depends upon the dimension of the problem, and numerical solutions of the governing partial differential equation are consistent with our calculations.

2020 Mathematics subject classification: 35Q79.

Keywords and phrases: reaction-diffusion, Fisher-Kolmogorov model, Fisher's equation, Stefan condition, moving boundary problem, travelling waves, invasion, extinction.

1. Introduction

The well-known Fisher–Kolmogorov model [7, 17, 20, 29, 36] is a reaction–diffusion equation that is often used to describe the spatial and temporal spreading of a population density where individuals in that population undergo random diffusive migration and logistic proliferation. The Fisher–Kolmogorov model is often written as

$$\frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u(x,t)}{\partial x^2} + \lambda u(x,t) \left[1 - \frac{u(x,t)}{K} \right],\tag{1.1}$$

where u(x, t) is the population density, x is the position, t is the time, D is the diffusivity, λ is the proliferation rate and K is the carrying capacity density. The Fisher–Kolmogorov equation is often studied on an infinite domain, $-\infty < x < \infty$, where

¹School of Mathematical Sciences, Queensland University of Technology, Brisbane, Queensland 4001, Australia; e-mail: matthew.simpson@qut.edu.au.

^{*}This is a contribution to the series of invited papers by past Tuck medallists (Editorial, Issue 62(1)).

Matthew J. Simpson was awarded the 2020 Tuck medal.

[©] Australian Mathematical Society 2020

it is well known to give rise to travelling wave solutions that eventually propagate with speed $c = 2\sqrt{D\lambda}$ for initial conditions with compact support [7, 17, 20, 29, 36]. The Fisher–Kolmogorov equation, and certain extensions, have been used to model invasion fronts in ecology [3, 4, 18, 44, 51, 52] and cell biology [5, 19, 22, 26– 28, 30, 31, 37, 38, 41, 43, 48–50, 53–55, 57–59]. Despite the widespread application of this fundamental model, there are several shortcomings. First, any localized initial condition with compact support will always lead to population growth and successful colonization. Therefore, an implicit assumption in the Fisher–Kolmogorov model is that the population will always survive and never go extinct. Second, solutions of the Fisher–Kolmogorov equation are smooth and without compact support. This means that the Fisher–Kolmogorov model does not, strictly speaking, lead to a clear and unambiguous invasion front. This can be problematic, because well-defined invasion fronts are often observed in practice [30, 31].

There are several ways that these two shortcomings of the Fisher–Kolmogorov model have been addressed in the applied mathematics literature. One common approach is to consider an extension of equation (1.1) that incorporates degenerate nonlinear diffusion, since this leads to travelling wave solutions with a well-defined front [1, 23, 30–32, 36, 39, 40, 42, 46, 60]. Another extension that has received less attention in the applied mathematics literature, but far more attention in the analysis literature, is to re-cast equation (1.1) as a moving boundary problem,

$$\frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u(x,t)}{\partial x^2} + \lambda u(x,t) \left[1 - \frac{u(x,t)}{K} \right], \tag{1.2}$$

on 0 < x < L(t), with $\partial u(0, t)/\partial x = 0$ and u(L(t), t) = 0, ensuring that there is a welldefined front at the moving boundary, x = L(t). To close the problem, the evolution of the moving boundary is taken to follow a classical Stefan condition [8, 21, 33–35],

$$\frac{dL(t)}{dt} = -\hat{\kappa}\frac{\partial u(L(t), t)}{\partial x}$$

As we will show, the adoption of equation (1.2) alleviates both the shortcomings of the classical Fisher–Kolmogorov model, since this moving boundary analogue leads to solutions with well-defined fronts, as well as permitting certain initial conditions to become extinct.

The moving boundary analogue of the Fisher–Kolmogorov model has been called the "Fisher–Stefan model" [15]. To simplify our analysis, we re-scale the variables: $x' = x/\sqrt{D/\lambda}$, $t' = t\lambda$ and u' = u/K. Dropping the prime notation gives

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} + u(x,t)[1-u(x,t)],\tag{1.3}$$

on 0 < x < L(t), with $\partial u(0, t)/\partial x=0$, and u(L(t), t) = 0 with $dL(t)/dt = -\kappa \partial u(L(t), t)/\partial x$. In this nondimensional framework there is just one parameter, $\kappa > 0$. Varying κ allows us to control the finite speed of the moving boundary at x = L(t). This mathematical model has been studied extensively in the analysis literature [6, 9–14]. Much of this analysis has centred upon proving properties of travelling wave solutions of equation (1.3) as well as characterizing the "spreading–vanishing dichotomy". As we will show, it is very interesting that certain initial conditions and choices of κ in equation (1.3) lead to eventual "spreading" in the form of a travelling wave, whereas other choices of initial conditions and κ in equation (1.3) lead to "extinction". A key feature of the spreading–vanishing dichotomy is that there exists a critical length, L_c , such that solutions of equation (1.3) that evolve in such a way that $L(t) > L_c$ always lead to eventual spreading, whereas solutions that evolve in such a way that $L(t) \neq L_c$ always lead to eventual extinction. A great deal of attention has been paid to the analysis of this spreading–vanishing dichotomy, and establishing that $L_c = \pi/2$ [6, 9–14].

The aim of this work is to revisit the spreading-vanishing dichotomy in a more general setting by re-casting equation (1.3) in a radially symmetric geometry. Using numerical simulations to guide our calculations, we provide a very straightforward interpretation of L_c and show how the critical length depends upon the dimension of the problem. All results are supported by numerical evidence. The details of the numerical scheme we use to solve equation (1.3) are described in Appendix A and MATLAB software to implement the numerical scheme and to explore and visualize various solutions is available at GitHub.

2. Results and discussion

We will revisit the spreading–vanishing dichotomy in a one-dimensional coordinate system before moving on to show that the calculations can be extended to higher dimensions.

2.1. Preliminary results in one dimension We first begin by visualizing numerical solutions of equation (1.3). For simplicity, all numerical solutions in this work have the same initial condition: u(x, 0) = 1 for $0 \le x \le 1$ with L(0) = 1. The solutions of equation (1.3) with $\kappa = 1$ are given in Figure 1(a)–(d), showing that the initial density evolves into a constant speed, constant shape travelling wave. Insights into such travelling waves can be obtained by phase plane analysis [15]. The evolution of L(t) is given in Figure 1(d), where we see that L(t) eventually increases linearly as $t \to \infty$.

With $\kappa = 0.2$, the solutions of equation (1.3) are given in Figure 1(e)–(h). These solutions show that the initial density evolves in such a way that the population goes extinct as $t \to \infty$. Solutions at t = 50 and t = 100 (Figure 1(f)–(g)) are plotted with an inset, because these solutions are so close to zero that it is impossible to clearly visualize the solutions when they are plotted on the same scale as the other solutions in Figure 1. The evolution of L(t) in Figure 1(h) shows that L(t) initially increases and then asymptotes to some constant value as $t \to \infty$. In this case, we always have $\partial u(x, t)/\partial x < 0$ at L(t) and so the Stefan condition ensures that $dL(t)/dt \ge 0$. This means that L(t) never decreases.

This simple numerical demonstration in Figure 1 illustrates the key features of the spreading–vanishing dichotomy. Unlike the usual Fisher–Kolmogorov model where



FIGURE 1. Numerical solutions of equation (1.3). Results in (a)–(d) are for $\kappa = 1$ and lead to a spreading travelling wave. Results in (e)–(h) are for $\kappa = 0.2$ and lead to extinction. (d) and (h) show the evolution of L(t) (blue) and $L_c = \pi/2$ (red). Colour available online.

all positive initial conditions eventually lead to spreading, here the moving boundary analogue of this model can either lead to an invading travelling wave or it can lead to extinction. Numerical solutions of equation (1.2) in Figure 1 provide some intuition about how we may analyse this dichotomy. As illustrated in Figure 1, when extinction occurs, we always have $u(x, t) \rightarrow 0$ as $t \rightarrow \infty$ for all $0 \le x \le L(t)$, suggesting that we can analyse the behaviour in this regime by linearizing. If $v(x, t) \ll 1$, an appropriate linear analogue of the Fisher–Stefan model is

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} + v(x,t)$$
(2.1)

on 0 < x < L(t) with $\partial v(0, t) / \partial x = 0$ and v(L(t), t) = 0. For the purposes of this analysis we treat the domain length as fixed, L(t) = L. The exact solution of equation (2.1) is

$$v(x,t) = \sum_{n=1}^{\infty} A_n \cos(\lambda_n x) e^{-t(\lambda_n^2 - 1)},$$
(2.2)

where $\lambda_n = \pi (2n - 1)/(2L)$ for n = 1, 2, 3, ... and the coefficients A_n can be chosen so that the solution matches an initial condition. As we will show, our analysis does not require that we specify these coefficients. We now approximate equation (2.2) by retaining just the first term in the series. Such leading eigenvalue approximations can be particularly accurate as $t \to \infty$ [24, 25, 45],

$$V(x,t) \sim A_1 \cos\left(\frac{\pi x}{2L}\right) e^{-t[(\pi/2L)^2 - 1]}.$$

With this solution we can specify a conservation statement for the time evolution of the total population in the domain,

$$\frac{dm}{dt} = \underbrace{\int_{0}^{L} V(x,t) \, dx}_{\text{accumulation due to source term}} - \underbrace{-\frac{\partial V(L,t)}{\partial x}}_{\text{loss due to the diffusive flux at } x = L}.$$
(2.3)

Setting dm/dt = 0, we solve (2.3) using V(x, t), giving $L_c = \pi/2 \approx 1.570796327$, which is independent of A_n . This means that whenever a solution of equation (1.3) evolves in such a way that $L(t) > \pi/2$, the accumulation due to the source term is greater than the loss due to the diffusive flux at the moving boundary. In contrast, whenever $L(t) < \pi/2$, the accumulation due to the source term is less than the loss at the moving boundary. This result has some interesting consequences and provides a straightforward explanation for our numerical results in Figure 1. For our initial condition we have $L(0) = 1 < \pi/2$ and it is unclear whether or not the transient solution will evolve such that $L(t) > \pi/2$ as $t \to \infty$. When κ is sufficiently large, we see that the evolution of the solution is such that L(t) eventually exceeds $\pi/2$ and at this point the population will continue to grow indefinitely, as shown in Figure 1(d). In contrast, for sufficiently small κ , the evolution of the solution is such that L(t) never reaches $\pi/2$ and so the diffusive flux out of the domain is greater than the production due to the source term and we see eventual extinction where $\lim_{t\to\infty} L(t) < \pi/2$, as shown in Figure 1(h).

Our numerical results and analysis of the linearized problem confirm that we have $L_c = \pi/2$ in one dimension and this explains our original choice of initial condition in Figure 1, where $L(0) = 1 < L_c$. In this case $L(0) < L_c$ and, without solving for the time-dependent solution, it is unclear whether L(t) evolves in such a way that it ever exceeds L_c . Therefore, with this initial condition we have the flexibility of choosing κ to be sufficiently small such that L(t) never reaches L_c and the population goes extinct, or we can choose κ to be sufficiently large such that L(t) will eventually exceed L_c and lead to a travelling wave. Had we chosen a different initial condition with $L(0) > L_c$, we would always observe the formation of a travelling wave provided $\kappa > 0$. Since we are interested in studying the spreading–extinction dichotomy, we restrict our numerical solutions to the case where $L(0) < L_c$. Setting L(0) = 1 is a convenient way to achieve this.

While it has long been known that $L_c = \pi/2$ in the more formal literature [6, 9–14], here we offer a very simple and intuitive way to calculate and interpret the spreading–vanishing dichotomy in terms of this critical length. Our approach is mathematically and conceptually straightforward and, as we will now show, also applies in other geometries.

2.2. Critical length in higher dimensions A generalization of equation (1.3) is to consider the Fisher–Stefan model in a radially symmetric coordinate system,

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} + \frac{d-1}{x} \frac{\partial u(x,t)}{\partial x} + u(x,t) [1 - u(x,t)]$$
(2.4)

for t > 0 and 0 < x < L(t), with $\partial u(0, t)/\partial x = 0$, u(L(t), t) = 0 and $dL(t)/dt = -\kappa \partial u(L(t), t)/\partial x$. Here d = 1, 2, 3 is the dimension. We will now explore how L_c depends upon d.

Setting d = 2 in equation (2.4) allows us to consider the spreading–vanishing dichotomy on a disc. Preliminary numerical simulations indicate that for a particular choice of u(x, 0) the solution may either evolve into a moving front when κ is sufficiently large, or the solution may go extinct when κ is sufficiently small, just like we demonstrated in Figure 1 when d = 1. To explore this, we linearize with $v(x, t) \ll 1$ to obtain

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} + \frac{1}{x} \frac{\partial v(x,t)}{\partial x} + v(x,t)$$
(2.5)

on 0 < x < L with $\partial v(0, t) / \partial x = 0$ and v(L, t) = 0. The exact solution of equation (2.5) is

$$v(x,t) = \sum_{n=1}^{\infty} A_n J_0 \left(x \sqrt{1 + \lambda_n^2} \right) e^{-\lambda_n^2 t},$$

where $J_0(x)$ is the zeroth-order Bessel function of the first kind [45]. Here the eigenvalues, λ_n , are obtained by setting $L\sqrt{1+\lambda_n^2}$ equal to the *n*th zeros of $J_0(x)$.

If we invoke a leading eigenvalue approximation, we have $\sqrt{1 + \lambda_1^2} = z/L$, where z is the first zero of $J_0(x)$, or $z \approx 2.404\,825\,558$. The leading eigenvalue approximation is

$$V(x,t) \sim A_1 J_0 \left(\frac{zx}{L}\right) e^{-t[(z/L)^2 - 1]}.$$
(2.6)

To proceed, we formulate a condition where the accumulation due to the source term is precisely matched by the loss at the moving boundary. Taking care to account for the geometry,

$$\underbrace{\int_{0}^{L} V(x,t) 2\pi x \, dx}_{\text{accumulation due to source term}} = \underbrace{-\frac{\partial V(L,t)}{\partial x} 2\pi L}_{\text{loss due to the diffusive flux at } x = L},$$

in which we can substitute equation (2.6) and solve for *L*. This procedure shows that L_c is the first zero of $J_0(x)$, giving $L_c \approx 2.404\,825\,558$. Numerical solutions in Figure 2 confirm this.

Setting d = 3 in equation (2.4), allows us to consider the spreading–vanishing dichotomy on a sphere. To explore the critical length, in this case we linearize with $v(x, t) \ll 1$, to obtain

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} + \frac{2}{x} \frac{\partial v(x,t)}{\partial x} + v(x,t)$$
(2.7)

on 0 < x < L with $\partial v(0, t) / \partial x = 0$ and v(L, t) = 0. The exact solution of equation (2.7)

$$v(x,t) = \sum_{n=1}^{\infty} \frac{A_n}{x} \sin\left(x\sqrt{1+\lambda_n^2}\right) e^{-\lambda_n^2 t},$$

where $\lambda_n = n\pi/L$, $n = 1, 2, 3, \dots$ The associated leading eigenvalue approximation is

$$V(x,t) \sim \frac{A_1}{x} \sin\left(\frac{\pi x}{L}\right) e^{-t[(\pi/L)^2 - 1]}.$$
 (2.8)

The associated conservation statement is

а

$$\underbrace{\int_{0}^{L} V(x,t) 4\pi x^{2} dx}_{\text{ccumulation due to source term}} = \underbrace{-\frac{\partial V(L,t)}{\partial x} 4\pi L^{2}}_{\text{loss due to the diffusive flux at } x = L},$$
(2.9)

in which we substitute equation (2.8) and solve for *L*, giving $L_c = \pi \approx 3.141592654$; numerical solutions in Figure 3 confirm this.

3. Conclusions

In this work, we explore an extension of the well-known Fisher–Kolmogorov model, called the Fisher–Stefan model. This extension involves reformulating the Fisher–Kolmogorov model as a moving boundary problem, and the evolution of the moving boundary is described by a classical Stefan condition. The Fisher–Stefan



FIGURE 2. Numerical solutions of equation (2.4) with d = 2. Results in (a)–(d) show a solution with $\kappa = 2.3$ leading to spreading. Results in (e)–(h) show a solution with $\kappa = 2.1$ leading to extinction. (d) and (h) show the evolution of L(t) (blue) and $L_c = 2.404 825 558$ (red). Colour available online.



FIGURE 3. Numerical solutions of equation (2.4) with d = 3. Results in (a)–(d) show a solution with $\kappa = 11$ leading to spreading. Results in (e)–(h) show a solution with $\kappa = 10$ leading to extinction. (d) and (h) show the evolution of L(t) (blue) and $L_c = \pi$ (red). Colour available online.

M. J. Simpson

model has two key advantages over the usual Fisher–Kolmogorov model: (i) solutions of the Fisher–Stefan model are characterized by a sharp front, which is often relevant in practice; (ii) solutions of the Fisher–Stefan model do not always lead to successful colonization, since the population can go extinct as $t \to \infty$. An important feature of the Fisher–Stefan model is the existence of a critical length, L_c . As we show, solutions of the Fisher–Stefan model that evolve in such a way that $L(t) > L_c$ always lead to spreading, whereas solutions that evolve in such a way that $L(t) \neq L_c$ always leads to extinction. Formal analysis of the spreading–vanishing dichotomy has established that $L_c = \pi/2$ in a standard one-dimensional Cartesian geometry [6, 9–14]. This property is often called the spreading–vanishing dichotomy and it has been extensively studied in one dimension. Far less attention has been paid to similar behaviour in higher dimensions.

We also reformulate the Fisher–Stefan model in a radially symmetric coordinate system, and study the spreading–vanishing dichotomy in one, two and three dimensions. Using simple conservation arguments, we confirm that $L_c = \pi/2$ in the usual one-dimensional geometry and this result is confirmed by numerical solutions. By extending these ideas to consider the Fisher–Stefan model on a disc and sphere, we find that the critical length depends upon the geometry of the problem. In particular, the critical length for the Fisher–Stefan model on a disc is the first zero of the zeroth-order Bessel function of the first kind ($L_c \approx 2.404\,825\,558$), and the critical length for the Fisher–Stefan model on a sphere is π ($L_c \approx 3.141\,592\,654$). Numerical solutions of the governing partial differential equation are consistent with these findings.

Our approach for calculating the critical length is conceptually straightforward and shows how the critical length depends upon the dimension. A great deal of literature about the spreading–vanishing dichotomy involves rigorous analysis that can be both difficult to interpret and difficult to extend to more general problems. Our approach, in contrast, is quite flexible and there are many potential extensions. While we have not pursued further calculations for other choices of *d*, it is straightforward to apply the methods described here for d > 3 to explore the spreading–vanishing dichotomy on an hypersphere. For example, setting d = 4 in equation (2.4) and repeating the analysis shows that the critical length is the first zero of the first-order Bessel function of the first kind ($L_c \approx 3.831705970$). Further calculations for different *d* can also be performed.

We close by commenting on some extensions of equation (2.4) that could be of interest. As we already pointed out in Section 1, a very common extension of the classical Fisher-Kolmogorov model is to generalize the linear diffusion term to a degenerate nonlinear diffusion term [1, 23, 30–32, 36, 39, 40, 42, 46, 60]. This generalization is often motivated by the desire to seek solutions with a welldefined sharp front. While it is certainly possible to generalize equation (2.4) to include degenerate nonlinear diffusion [16], an important consequence of this in the moving boundary context is that this extension does not lead to a spreadingvanishing dichotomy. This is because the flux at the moving boundary x = L(t), where u(L(t), t) = 0, is always zero, thereby always preventing extinction. In contrast, the one-phase Stefan condition in equation (2.4) leads to a loss of mass at the moving boundary, and it is this loss of mass that enables the population to go extinct. Another interesting extension would be to consider the spreading-vanishing dichotomy in higher dimensions for nonradial geometries, and explore the relationship between the solutions in radial and nonradial geometries [2, 56]. Such an extension to consider moving boundary problems in higher dimensions without radial symmetry would require a very different approach numerically and so we leave this for future consideration.

A. Appendix: Numerical methods

We develop a simple, robust numerical solution of

$$\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} + \frac{d-1}{x} \frac{\partial u(x,t)}{\partial x} + u(x,t)[1-u(x,t)]$$

for t > 0 and 0 < x < L(t) with u(L(t), t) = 0, $\partial u(0, t)/\partial x = 0$ and $dL(t)/dt = -\kappa \partial u(L(t), t)/\partial x$. To solve this partial differential equation, we first re-cast the moving boundary problem on a fixed domain by setting $\xi = x/L(t)$, giving

$$\frac{\partial u(\xi,t)}{\partial t} = \frac{1}{L^2(t)} \frac{\partial^2 u(\xi,t)}{\partial \xi^2} + \left[\frac{\xi}{L(t)} \frac{dL(t)}{dt} + \frac{d-1}{\xi L^2(t)}\right] \frac{\partial u(\xi,t)}{\partial \xi} + u(\xi,t)[1-u(\xi,t)] \quad (A.1)$$

for t > 0 and $0 < \xi < 1$ with u(1, t) = 0, $\partial u(0, t)/\partial \xi = 0$ and $dL(t)/dt = -(\kappa/L(t))\partial u(1, t)/\partial \xi$.

We discretize equation (A.1) on a uniform mesh with spacing $\Delta \xi$, and the value of $u(\xi, t)$ at each node is indexed with a subscript i = 1, 2, 3, ..., N, where $N = 1/\Delta \xi + 1$. Integrating through time using an implicit Euler approximation, using a subscript *m* to denote the time step, leads to the following system of *N* nonlinear algebraic equations [47],

$$u_1^m = u_2^m,$$

$$\frac{u_i^m - u_i^{m-1}}{\Delta t} = \frac{(u_{i-1}^m - 2u_i^m + u_{i+1}^m)}{(\Delta \xi L^m)^2} + \left[\frac{\xi_i}{L^m}\frac{dL^m}{dt} + \frac{d-1}{\xi_i(L^m)^2}\right]\frac{(u_{i+1}^m - u_{i+1}^m)}{2\Delta \xi} + u_i^m[1 - u_i^m], \quad i = 2, 3, 4, \dots, N-1,$$

$$u_N^m = 0,$$

where $dL^m/dt = \kappa u_{N-1}^m/(L^m\Delta\xi)$. This system of nonlinear algebraic equations is solved using Newton–Raphson iteration until the change in estimates of u_i^m per iteration falls below a tolerance of ε . This algorithm provides estimates of $u(\xi, t)$ on $0 < \xi < 1$, which are then re-scaled to give u(x, t) on 0 < x < L(t). A MATLAB implementation of this algorithm is available at GitHub. All results presented in this work use $\Delta\xi = 1 \times 10^{-3}$, $\Delta t = 1 \times 10^{-4}$ and $\varepsilon = 1 \times 10^{-10}$. This choice of discretization appears to be suitable for our purposes, but numerical results should always be checked to test that they are independent of the mesh. Experience suggests that problems with larger κ require particular care to ensure grid convergence.

Acknowledgements

This work was supported by the Australian Research Council (DP170100474). I appreciate many informal discussions on this topic with Scott McCue, Yihong Du, Wang Jin and Maud El-Hachem, together with helpful suggestions of three anonymous referees.

References

- R. E. Baker and M. J. Simpson, "Models of collective cell motion for cell populations with different aspect ratio: diffusion, proliferation and travelling waves", *Physica A* **391** (2012) 3729–3750; doi: 10.1016/j.physa.2012.01.009.
- G. I. Barenblatt, Scaling, self-similarity, and intermediate asymptotics (Cambridge University Press, Cambridge, 1996); doi: 10.1017/CBO9781107050242.
- [3] B. H. Bradshaw-Hajek and P. Broadbridge, "A robust cubic reaction-diffusion system for gene propagation", 39 (2004) 1151–1163; doi: 10.1016/S0895-7177(04)90537-7.
- [4] P. Broadbridge, B. H. Bradshaw, G. R. Fulford and G. K. Aldis, "Huxley and Fisher equations for gene propagation: an exact solution", *ANZIAM J.* 44 (2002) 11–20; doi: 10.1017/S1446181100007860.
- [5] A. Browning, P. Haridas and M. J. Simpson, "A Bayesian sequential learning framework to parameterise continuum models of melanoma invasion into human skin", *Bull. Math. Biol.* 81 676–698; doi: 10.1007/s11538-018-0532-1.
- [6] G. Bunting, Y. Du and K. Krakowski, "Spreading speed revisited: analysis of a free boundary model", *Netw. Heterog. Media* 7 (2012) 583–603; doi: 10.3934/nhm.2012.7.583.
- J. Canosa, "On a nonlinear diffusion equation describing population growth", *IBM J. Res. Dev.* 17 (1973) 307–313; doi: 10.1147/rd.174.0307.
- [8] J. Crank, Free and moving boundary problems (Oxford University Press, Oxford, 1987).
- [9] Y. Du and Z. Guo, "Spreading–vanishing dichotomy in a diffusive logistic model with a free boundary, II", J. Differential Equations 250 (2011) 4336–4366; doi: 10.1016/j.jde.2011.02.011.
- [10] Y. Du and Z. Guo, "The Stefan problem for the Fisher–KPP equation", J. Differential Equations 253 (2012) 996–1035; doi: 10.1016/j.jde.2012.04.014.
- [11] Y. Du and Z. Lin, "Spreading-vanishing dichotomy in the diffusive logistic model with a free boundary", *SIAM J. Math. Anal.* 42 (2010) 377–405; doi: 10.1137/090771089.
- [12] Y. Du and B. Lou, "Spreading and vanishing in nonlinear diffusion problems with free boundaries", J. Eur. Math. Soc. 17 (2015) 2673–2724; doi: 10.4171/JEMS/568.
- [13] Y. Du, H. Matano and K. Wang, "Regularity and asymptotic behavior of nonlinear Stefan problems", Arch. Ration. Mech. Anal. 212 (2014) 957–1010; doi: 10.1007/s00205-013-0710-0.
- [14] Y. Du, H. Matsuzawa and M. Zhou, "Sharp estimate of the spreading speed determined by nonlinear free boundary problems", *SIAM J. Math. Anal.* 46 (2014) 375–396; doi: 10.1137/130908063.
- [15] M. El-Hachem, S. W. McCue, W. Jin, Y. Du and M. J. Simpson, "Revisiting the Fisher– Kolmogorov–Petrovsky–Piskunov equation to interpret the spreading–extinction dichotomy", *Proc. R. Soc. Lond. Ser. A: Math. Phys. Eng. Sci.* 475 (2019) 20190378; doi: 10.1098/rspa.2019.0378.
- [16] N. T. Fadai and M. J. Simpson, "New travelling wave solutions for the porous-Fisher model with a moving boundary", J. Phys. A: Math. Theor. 53 (2020) 095601; doi: 10.1088/1751-8121/ab6d3c.
- [17] R. A. Fisher, "The wave of advance of advantageous genes", Ann. Eugen. 7 (1937) 355–369; doi: 10.1111/j.1469-1809.1937.tb02153.x.
- [18] L. K. Forbes, "A two-dimensional model for large-scale bushfire spread", J. Aust. Math. Soc. Ser. B: Appl. Math. (currently, ANZIAM J.) 39 (1997) 171–194; doi: 10.1017/S0334270000008791.
- [19] R. A. Gatenby and E. T. Gawlinski, "A reaction–diffusion model of cancer invasion", *Cancer Res.* 56 (1996) 5745–5753; https://cancerres.aacrjournals.org/content/56/24/5745.article-info.

- [20] P. Grindrod, *Patterns and waves* (Oxford University Press, Oxford, 2007); doi: 10.1137/1035173.
- [21] S. C. Gupta, The classical Stefan problem. Basic concepts, modelling and analysis with quasianalytical solutions and methods. 2nd edn (Elsevier, Amsterdam, 2017); doi: 10.1016/C2017-0-02306-6.
- [22] P. Haridas, C. J. Penington, J. A. McGovern, D. L. S. McElwain and M. J. Simpson, "Quantifying rates of cell migration and cell proliferation in co-culture barrier assays reveals how skin and melanoma cells interact during melanoma spreading and invasion", *J. Theoret. Biol.* **423** (2017) 13–25; doi: 10.1016/j.jtbi.2017.04.017.
- [23] S. Harris, "Fisher equation with density-dependent diffusion: special solutions", J. Phys. A: Math. Theor. 37 (2004) 6267–6268; doi: 10.1088/0305-4470/37/24/005.
- [24] R. I. Hickson, S. I. Barry and G. N. Mercer, "Critical times in multilayer diffusion. Part 1: Exact solutions", *Int. J. Heat Mass Transfer* 52 (2009) 5776–5783; doi: 10.1016/j.ijheatmasstransfer.2009.08.013.
- [25] R. I. Hickson, S. I. Barry and G. N. Mercer, "Critical times in multilayer diffusion. Part 2: Approximate solutions", *Int. J. Heat Mass Transfer* 52 (2009) 5784–5791; doi: 10.1016/j.ijheatmasstransfer.2009.08.012.
- [26] W. Jin, E. T. Shah, C. J. Penington, S. W. McCue, L. K. Chopin and M. J. Simpson, "Reproducibility of scratch assays is affected by the initial degree of confluence: experiments, modelling and model selection", *J. Theoret. Biol.* **390** (2016) 136–145; doi: 10.1016/j.jtbi.2015.10.040.
- [27] S. T. Johnston, J. V. Ross, B. J. Binder, D. L. S. McElwain, P. Haridas and M. J. Simpson, "Quantifying the effect of experimental design choices for in vitro scratch assays", *J. Theoret. Biol.* 400 (2016) 19–31; doi: 10.1016/j.jtbi.2016.04.012.
- [28] S. T. Johnston, E. T. Shah, L. K. Chopin, D. L. S. McElwain and M. J. Simpson, "Estimating cell diffusivity and cell proliferation rate by interpreting IncuCyte ZOOMTM assay data using the Fisher–Kolmogorov model", *BMC Syst. Biol.* 9 (2015) 38, 1–12; doi: 10.1186/s12918-015-0182-y.
- [29] A. N. Kolmogorov, I. G. Petrovskii and N. S. Piskunov, "A study of the diffusion equation with increase in the amount of substance, and its application to a biological problem", *Moscow Univ. Math. Bull.* 1 (1937) 1–26.
- [30] P. K. Maini, D. L. S. McElwain and D. I. Leavesley, "Traveling wave model to interpret a wound-healing cell migration assay for human peritoneal mesothelial cells", *Tissue Eng.* 10 (2004) 475–482; doi: 10.1089/107632704323061834.
- [31] P. K. Maini, D. L. S. McElwain and D. Leavesley, "Travelling waves in a wound healing assay", *Appl. Math. Lett.* **17** (2004) 575–580; doi: 10.1016/S0893-9659(04)90128-0.
- [32] S. W. McCue, W. Jin, T. J. Moroney, K.-Y. Lo, S. E. Chou and M. J. Simpson, "Hole-closing model reveals exponents for nonlinear degenerate diffusivity functions in cell biology", *Physica D* 398 (2019) 130–140; doi: 10.1016/j.physd.2019.06.005.
- [33] S. W. McCue, J. R. King and D. S. Riley, "Extinction behaviour for two-dimensional inwardsolidification problems", *Proc. R. Soc. Lond. Ser. A: Math. Phys. Eng. Sci.* 459 (2003) 977–999; doi: 10.1098/rspa.2002.1059.
- [34] S. W. McCue, J. R. King and D. S. Riley, "The extinction problem for three-dimensional inward solidification", J. Engrg. Math. 52 (2005) 389–409; doi: 10.1007/s10665-005-3501-2.
- [35] S. W. McCue, B. Wu and J. M. Hill, "Classical two-phase Stefan problem for spheres", Proc. R. Soc. Lond. Ser. A: Math. Phys. Eng. Sci. 464 (2008) 2055–2076; doi: 10.1098/rspa.2007.0315.
- [36] J. D. Murray, Mathematical biology I. An introduction (Springer, New York, 2002); doi: 10.1007/b98868.
- [37] J. T. Nardini, D. A. Chapnick, X. Liu and D. M. Bortz, "Modeling keratinocyte wound healing dynamics: cell-cell adhesion promotes sustained collective migration", *J. Theoret. Biol.* 400 (2016) 103–117; doi: 10.1016/j.jtbi.2016.04.015.

[13]

M. J. Simpson

- [38] K. J. Painter and J. A. Sherratt, "Modelling the movement of interacting cell populations", J. Theoret. Biol. 225 (2003) 327–339; doi: 10.1016/S0022-5193(03)00258-3.
- [39] F. Sánchez Garduno and P. K. Maini, "An approximation to a sharp type solution of a densitydependent reaction diffusion equation", *Appl. Math. Lett.* 7 (1994) 47–51; doi: 10.1016/0893-9659(94)90051-5.
- [40] F. Sánchez Garduno and P. K. Maini, "Traveling wave phenomena in some degenerate reaction diffusion equations", J. Differential Equations 117 (1994) 281–319; doi: 10.1006/jdeq.1995.1055.
- [41] B. G. Sengers, C. P. Please and R. O. C. Oreffo, "Experimental characterization and computational modelling of two-dimensional cell spreading for skeletal regeneration", *J. R. Soc. Interface* 4 (2007) 1107–1117; doi: 10.1098/rsif.2007.0233.
- [42] J. A. Sherratt and B. P. Marchant, "Nonsharp travelling wave fronts in the Fisher equation with degenerate nonlinear diffusion", *Appl. Math. Lett.* 9 (1996) 33–38; doi: 10.1016/0893-9659(96)00069-9.
- [43] J. A. Sherratt and J. D. Murray, "Models of epidermal wound healing", Proc. R. Soc. Lond. Ser. B 241 (1990) 29–36; doi: 10.1098/rspb.1990.0061.
- [44] N. Shigesada, K. Kawasaki and Y. Takeda, "Modeling stratified diffusion in biological invasions", *American Naturalist* 146 (1995) 229–251; doi: 10.1086/285796.
- [45] M. J. Simpson and R. E. Baker, "Exact calculations of survival probability for diffusion on growing lines, disks and spheres: the role of dimension", *J. Chem. Phys.* 143 (2015) 094109; doi: 10.1063/1.4929993.
- [46] M. J. Simpson, R. E. Baker and S. W. McCue, "Models of collective cell spreading with variable cell aspect ratio: a motivation for degenerate diffusion models", *Phys. Rev. E* 83 (2011) 021901; doi: 10.1103/PhysRevE.83.021901.
- [47] M. J. Simpson, K. A. Landman and T. P. Clement, "Assessment of a non-traditional operator split algorithm for simulation of reactive transport", *Math. Comput. Simul.* **70** (2005) 44–60; doi: 10.1016/j.matcom.2005.03.019.
- [48] M. J. Simpson, K. A. Landman, B. D. Hughes and D. F. Newgreen, "Looking inside an invasion wave of cells using continuum models: proliferation is the key", *J. Theoret. Biol.* 243 (2006) 343–360; doi: 10.1016/j.jtbi.2006.06.021.
- [49] M. J. Simpson, K. K. Treloar, B. J. Binder, P. Haridas, K. J. Manton, D. I. Leavesley, D. L. S. McElwain and R. E. Baker, "Quantifying the roles of motility and proliferation in a circular barrier assay", *J. R. Soc. Interface* **10** (2013) 20130007; doi: 10.1098/rsif.2013.0007.
- [50] M. J. Simpson, D. C. Zhang, M. Mariani, K. A. Landman and D. F. Newgreen, "Cell proliferation drives neural crest cell invasion of the intestine", *Dev. Biol.* **302** (2007) 553–568; doi: 10.1016/j.ydbio.2006.10.017.
- [51] J. G. Skellam, "Random dispersal in theoretical populations", *Biometrika* 38 (1951) 196–218; doi: 10.2307/2332328.
- [52] J. Steele, J. Adams and T. Sluckin, "Modelling paleoindian dispersals", *World Archaeol.* 30 (1998) 286–305; doi: 10.1080/00438243.1998.9980411.
- [53] K. R. Swanson, C. Bridge, J. D. Murray and E. C. Alvord Jr, "Virtual and real brain tumors: using mathematical modeling to quantify glioma growth and invasion", *J. Neurol. Sci.* 216 (2003) 1–10; doi: 10.1016/j.jns.2003.06.001.
- [54] K. R. Swanson, R. C. Rostomily and E. C. Alvord Jr, "A mathematical modelling tool for predicting survival of individual patients following resection of glioblastoma: a proof of principle", *Br. J. Cancer* **98** (2008) 113–119; doi: 10.1038/sj.bjc.6604125.
- [55] K. K. Treloar, M. J. Simpson, D. L. S. McElwain and R. E. Baker, "Are *in vitro* estimates of cell diffusivity and cell proliferation rate sensitive to assay geometry?", *J. Theoret. Biol.* 356 (2014) 71–84; doi: 10.1016/j.jtbi.2014.04.026.
- [56] J. L. Vázquez, *The porous medium equation* (Oxford University Press, Oxford, 2007); doi: 10.1093/acprof:oso/9780198569039.001.0001.

Critical length in higher dimensions

- [57] S. T. Vittadello, S. W. McCue, G. Gunasingh, N. K. Haass and M. J. Simpson, "Mathematical models for cell migration with real-time cell cycle dynamics", *Biophys. J.* 114 (2018) 1241–1253; doi: 10.1016/j.bpj.2017.12.041.
- [58] B. N. Vo, C. C. Drovandi, A. N. Pettitt and M. J. Simpson, "Quantifying uncertainty in parameter estimates for stochastic models of collective cell spreading using approximate Bayesian computation", *Math. Biosci.* 263 (2015) 133–142; doi: 10.1016/j.mbs.2015.02.010.
- [59] D. J. Warne, R. E. Baker and M. J. Simpson, "Using experimental data and information criteria to guide model selection for reaction–diffusion problems in mathematical biology", *Bull. Math. Biol.* 81 (2019) 1760–1804; doi: 10.1007/s11538-019-00589-x.
- [60] T. P. Witelski, "Merging traveling waves for the porous-Fisher's equation", *Appl. Math. Lett.* 8 (1995) 57–62; doi: 10.1016/0893-9659(95)00047-T.

[15]