Tactically-driven nonmonotone travelling waves

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Abstract

Models of cell invasion incorporating directed cell movement up a gradient of an external substance and carrying capacity-limited proliferation give rise to travelling wave solutions. Travelling wave profiles with various shapes, including smooth monotonically decreasing, shock-fronted nonmonotone shapes, have been reported previously in the literature. The existence of tactically-driven shock-fronted nonmonotone travelling wave solutions is analysed for the first time. We develop a necessary condition for nonmonotone shock-fronted solutions. This condition shows that some of the previously reported shock-fronted nonmonotone solutions are genuine while others are a consequence of numerical error. Our results demonstrate that, for certain conditions, travelling wave solutions can be either smooth and monotone, smooth and nonmonotone or discontinuous and nonmonotone. These different shapes correspond to different invasion speeds. A necessary and sufficient condition for the travelling wave with minimum wave speed to be nonmonotone is presented. Several common forms of the tactic sensitivity function have the potential to satisfy the newly developed condition for nonmonotone shock-fronted solutions developed in this work.

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1. Introduction

Fisher’s equation is an archetypal mathematical model in theoretical biology that has had an impact on the discipline for over three decades [4,5,10,14]. This equation can be interpreted as a one-dimensional representation of cell invasion that includes cell motility generated by a random walk and cell proliferation governed by a logistic growth model. Fisher’s equation exhibits travelling wave solutions that have been extensively studied since they may be used to represent cell invasion fronts [10,20]. Of particular interest in the context of this work is the observation that travelling wave solutions of Fisher’s equation are monotonically shaped [2,14].

Cell motility can be directed by extracellular environmental gradients rather than a random walk. Gradient-mediated motility, such as chemotaxis or haptotaxis, is usually modelled with a nonlinear advection term to represent the movement of cells directed up a gradient of attractant or adhesion sites respectively [1,5,7,8,12,14,15,20]. Cell motility governed by chemotactic and haptotactic responses are relevant for malignant tumour invasion [12,13,15] and developmental cell migrations that occur during embryogenesis [7,8,19,20].

A canonical form of a one-dimensional continuum model of tactically-driven cell migration is given by Eqs. (1) and (2), where \( n(x,t) \) is cell density and \( g(x,t) \) is the concentration of the attractant or adhesion site density, at position \( x \) and time \( t \):

\[
\frac{\partial g}{\partial t} = h(g,n), \quad (1)
\]

\[
\frac{\partial n}{\partial t} = -\frac{\partial}{\partial x}\left(n\chi(g)\frac{\partial g}{\partial x}\right) + f(g,n). \quad (2)
\]

The tactic sensitivity function, \( \chi(g) > 0 \), represents the attractive strength of the cell’s tactic response. Typically \( \chi(g) \) is assumed to be a constant or a simple decreasing function to represent saturation effects [14]. The functions \( h \) and \( f \)
and are readily (1) 12
Fig. 1 (2) 17 8. Our analysis is focused on tactically-
have the capacity to exhibit nonmonotone (b) shows a
Fig. 1 (a) Fig. 1 (2) Fig. 1. The profile in Fig. 1(a) shows a nonmonotone invasion wave where the nonmonotone shape is driven by the kinetic functions. Fig. 1(b) shows a monotone invasion wave, while Fig. 1(c) shows a nonmonotone invasion wave where the nonmonotone shape is driven by the tactic term. The analysis presented here differentiates between and explains the origins of the dissimilar invasion shapes summarized in Fig. 1. Our analysis is focused on tactically-driven nonmonotone profiles rather than kinetically-generated nonmonotone profiles. Our numerical results are carefully constructed using a high-resolution central scheme so that the profiles are free from artificial oscillations.

In summary, we will show that tactic cell invasion systems of the form (1) and (2) have the capacity to exhibit nonmonotone travelling wave solutions. The conditions under which such nonmonotone travelling waves exist are explored. These new conditions are used to reexamine profiles reported previously in the literature, confirming that some of the nonmonotone solutions are real whereas others are caused by numerical error.

2. Travelling wave analysis

We are interested in the biologically relevant case where the cell population depletes an initial uniform tactic concentration. Therefore we consider a general class of problems where there are two possible spatially homogeneous steady states corresponding to \( f = h = 0 \). Without any loss of generality, we suppose the system has been scaled so that the uninvaded state corresponds to \( (g, n) = (1, 0) \) and the invaded state corresponds to \( (g, n) = (0, 1) \). Therefore the kinetic functions satisfy

\[
\begin{align*}
  f(1, 0) &= h(1, 0) = 0, \\
  f(0, 1) &= h(0, 1) = 0.
\end{align*}
\]

In order to write the system in this form, the cell density must be scaled so that \( n = 1 \) corresponds to the invaded state. Furthermore, we require the cell density to satisfy \( n \geq 0 \) to be physically realistic.

For arbitrary \( f \) and \( h \), an invasion wave is a solution that connects the invaded steady state \( n = 1 \) to the uninvaded state \( n = 0 \). Travelling wave solutions of (1) and (2) are sought connecting these two steady states. These solutions are investigated using both the phase plane and numerical simulations.
We consider travelling waves where the tactic concentration \( g \) is a monotonically increasing function of \( x \). This is equivalent to \( g \) being a monotonically decreasing function of \( t \) for a fixed \( x \). Such travelling waves are consistent with the requirement that the cell population depletes a tactic concentration as it moves into uninvaded territory. From Eq. (1), this implies that solutions satisfy \( h(g, n) < 0 \) in the neighbourhood of the trajectory joining the two steady states.

Two tactic invasion systems have been extensively studied with particular reference to their potential to support travelling wave solutions. Here their potential to support nonmonotone travelling waves is addressed for the first time. The first system modelled a chemotactic cell invasion process associated with the development of the enteric nervous system during vertebrate embryogenesis [19,20]. For this problem \( n(x, t) \) represents the invading cell density and \( g(x, t) \) is an attractant concentration. The kinetic terms, transformed so that the \((g, n)\) steady states are \((0, 1)\) and \((1, 0)\), correspond to

\[
f(g, n) = n(1 - n), \quad h(g, n) = \beta(1 - g - n) - \gamma gn. \tag{4}
\]

The second system models haptotactic invasion of tumor cells with density \( n(x, t) \), where \( g(x, t) \) represents the density of extracellular matrix (ECM) [11–13,15]. This model has kinetic functions given by

\[
f(g, n) = n(1 - n), \quad h(g, n) = -g^2 n. \tag{5}
\]

In our analysis, \( f \) and \( h \) are kept as arbitrary functions, such that \( h < 0 \) in the neighbourhood of the trajectory joining the invaded and uninvaded states. However, to maintain clarity specific examples of interest relevant to the commonly studied kinetics (4) and (5) are discussed in later sections.

Introducing the travelling wave coordinate for right-moving travelling waves \( z = x - ct \), where \( c > 0 \) is the dimensionless wave speed, the conservation system (1) and (2) can be written as a system of first order ordinary differential equations on \( -\infty < z < \infty \) as

\[
-c \frac{dg}{dz} = h(g, n), \tag{6}
\]

\[
-c \frac{dn}{dz} = -\frac{d}{dz} \left( \chi(g) n \frac{dg}{dz} \right) + f(g, n). \tag{7}
\]

These equations are combined and rearranged as

\[
\frac{dg}{dz} = H(g, n), \tag{8}
\]

\[
W(g, n) \frac{dn}{dz} = F(g, n), \tag{9}
\]

where

\[
H(g, n) = -\frac{h}{c}, \tag{10}
\]

\[
W(g, n) = 1 + \frac{\chi}{c^2} (h + nh_n), \tag{11}
\]

\[
F(g, n) = -\frac{1}{c} \left[ f - nh \left( \frac{\chi}{c^2} h \right)_g \right]. \tag{12}
\]

The independent variable dependence on \( \chi, f, h \) and \( \chi' = \frac{d\chi}{dg} \) has been dropped and subscript notation is used to denote partial differentiation.

In the \((g, n)\) phase plane, the \( n \)-nullcline is given by \( F(g, n) = 0 \), provided \( W(g, n) \neq 0 \) simultaneously. In fact the derivative \( dn/dz \) is undefined for points where \( W(g, n) = 0 \). These points are referred to as a "wall of singularities" [16,17]. A solution approaching a wall of singularities is unable to cross the wall unless it passes through a special point, called a hole in the wall, where both \( W(g, n) = 0 \) and \( F(g, n) = 0 \). Hence a hole in the wall is determined by the intersection points of the wall and any \( n \)-nullcline. For this system, trajectories can pass through a hole in the wall, denoted \((g_H, n_H)\). The slope of the trajectory at the hole is finite, determined using a series expansion of \( F(g, n)/W(g, n) \) about \((g_H, n_H)\).

### 2.1. Stability of the steady states

The stability of the steady states determines whether there is a trajectory in the phase plane which connects the two steady state solutions.

First we return to the system (1) and (2) and discuss the stability of the steady states in the kinetic model, where \( t \) is the independent variable. The stability of a steady state to spatially uniform perturbations is determined by the eigenvalues \( \lambda \) of the Jacobian matrix

\[
J = \begin{bmatrix} h_g & h_n \\ f_g & f_n \end{bmatrix}, \tag{13}
\]

evaluated at a steady state. The eigenvalues satisfy \( \lambda^2 = Tr(J) \lambda + Det(J) = 0 \). If \( Det(J) < 0 \) then a steady state is unstable (saddle); otherwise if \( Det(J) > 0 \) then a steady state is unstable (node or spiral) for \( Tr(J) > 0 \) or stable (node or spiral) for \( Tr(J) < 0 \).

For a trajectory to join \((1, 0)\) to \((0, 1)\) as \( t \) increases, we require \((1, 0)\) to be either a saddle or an unstable node (given that \( n \leq 0 \) is required), while \((0, 1)\) must be either a saddle or a stable node or spiral. We are interested in the case of tactically-driven nonmonotone travelling waves. Therefore, since the travelling wave system (8)–(12) relaxes to the purely kinetic system \( dn/dg = f(g, n)/W(g, n) \) in the limit as the wave speed \( c \rightarrow \infty \) for any positive \( \chi(g) \) [2], the dynamics of the kinetic problem require that both \( n(t) \) and \( g(t) \) be monotonic functions. We are not concerned here with the alternate case where the dynamics of \( f \) and \( h \) generate nonmonotone solutions. We will refer to this alternative kind of nonmonotone solution as a kinetically-generated nonmonotone solution. This kind of solution was illustrated in Fig. 1(a). Further details of the analysis of the kinetic model are outlined in Appendix A.

We now consider how the inclusion of the taxis term affects the stability of a steady state of the system (1) and (2). The travelling wave coordinate system (8) and (9) has a singularity at \( W(g, n) = 0 \). To avoid this singularity, it is convenient to regularize the equations by introducing the variable \( Z \), where \( dZ/dz = W(g, n)/dW/dg [7,13,17] \). Then writing \( g(z) = G(Z) \) and \( n(z) = N(Z) \), the system (8) and (9) transforms to \( Z \)-space...
as
\[
\frac{dG}{dZ} = H(G, N) W(G, N), \quad \frac{dN}{dZ} = F(G, N).
\]

The steady states of the kinetic system, defined by points where \( f(g, n) = h(g, n) = 0 \), also satisfy \( F(g, n) = H(g, n) = 0 \). Hence \((1, 0)\) or \((0, 1)\) are steady states in the Z-space system. Furthermore, there are additional Z-space steady states given by points where both \( W = F = 0 \). These are just the holes in the wall of the Z-space problem, namely \((g_1, n_1)\), defined by \( F(g_1, n_1) = W(g_1, n_1) = 0 \).

Computing the Jacobian for this system yields
\[
K = \begin{bmatrix}
H_G W + H W_G & H_N W + H W_N \\
F_G & F_N
\end{bmatrix}.
\]

Simple algebraic manipulations determine the relationships \( \text{Tr}(K) = -\text{Tr}(J)/c \) and \( \text{Det}(K) = W \text{Det}(J)/c^2 \) at the steady states.

Consider the two steady states \((1, 0)\) or \((0, 1)\). In the kinetic system, the stability of these points is determined by \( \text{Det}(J) \) and \( \text{Tr}(J) \). In the transformation to the travelling wave coordinates, the sign of \( t \) is reversed, so that the sign on \( \text{Tr}(K) \) is opposite to the sign of \( \text{Tr}(J) \). The sign on \( \text{Det}(K) \) depends on which side of the wall the steady state lies (through the regularization from \( z \) to Z-space). Therefore if parameter variation causes the steady state to cross the wall, in the regularized variable \( Z \) the steady state of the original system changes type (from a saddle to either a node or spiral or vice versa). For example, suppose the point \((0, 1)\) is a node and the point \((1, 0)\) is a saddle when they are on the same side of the wall. A trajectory joining an unstable node to a saddle is required. As the parameters are changed (for example, reducing the wave speed \( c \)), the wall may move so that the point \((0, 1)\) is now on the opposite side of the wall. In this case, the point \((0, 1)\) is a saddle — a trajectory joining two saddle points is sought. Such a Z-space bifurcation phenomenon always involves the steady state crossing the wall via the hole in the wall. However, it is important to note that this phenomenon does not always occur and for some cases the two steady states remain on the same side of the wall for all possible wave speeds.

The nature of the interaction between the wall and the n-nullcline determines the stability of a hole in the wall in Z-space; the details are given in Appendix B.

3. Computational methods

3.1. Numerical solution of the partial differential equations

To numerically simulate travelling waves we solve (1) and (2) on \( 0 < x < L \) where \( L \) is large to avoid boundary effects. Zero flux conditions are imposed at \( x = 0 \). The minimum wave speed solutions can be obtained for any initial condition \( n(x, 0) \) with semi-compact support [8]. Travelling waves with \( c > c_{\text{min}} \) are obtained with an initial condition which has a sufficiently slowly exponentially decaying leading edge [8].

Numerical solutions are obtained by discretizing (1) and (2) with a high-accuracy central scheme [6]. Details of the discretization are a straightforward extension of previous applications [19]. Uniform spatial and temporal discretizations are chosen to give grid independent results. At each time step the location of a contour \( n(x, t) = \bar{n} \) is found and used to approximate the wave speed \( c \). The algorithm is executed until \( c \) settles to a constant.

3.2. Generating the phase plane

The equations (8) and (9) define a system of two autonomous ordinary differential equations. The location of the wall, n-nullcline, steady states and direction vectors defining any trajectory are known exactly for any given \( c \). The required trajectory joining the steady states is generated using standard numerical ordinary differential equation routines implemented in Mathematica, with the initial point determined iteratively.

4. Existence of smooth and discontinuous travelling wave solutions

Here we summarize results regarding the existence of travelling wave solutions to a general system of the type (1) and (2). These have been analysed by Perumpanani et al. [15], Marchant et al. [11–13] and Landman et al. [7] using phase plane analysis, hyperbolic partial differential equation theory, Rankine–Hugoniot jump conditions and the Lax entropy condition. A trajectory in the \((g, n)\) phase plane which connects \((0, 1)\) to \((1, 0)\) is required. Previous theoretical work has focused on the case when \( \chi(g) \) was a constant. Here we extend this to the case when \( \chi(g) \) varies with \( g \).

To demonstrate the results we choose an example with kinetic functions (4) and \( \chi(g) = 1 \) for a fixed set of parameters over a range of wave speeds. Fig. 2 illustrates results with the wave speed decreasing down the page. Note that for continuous solutions the travelling wave profiles have been shifted so that \( n(0, t) = 0.5 \). For the case where the solutions contain a discontinuity the profiles have been shifted so that the discontinuity is located at \( x = 0 \).

There exists a critical value of the wave speed \( c = c_{\text{crit}} \) such that for sufficiently large wave speed \( c > c_{\text{crit}} \), the two steady states are on the same side of the wall and the wall does not interfere with the trajectory joining the two steady states. There is a smooth trajectory connecting these two states, as demonstrated in Fig. 2(a). Hence \( c = c_{\text{crit}} \) marks the disappearance of a smooth trajectory joining the two steady states. There are two possible situations.

The steady states are on same side of the wall and \( c_{\text{crit}} \) is defined as the value of the wave speed where the trajectory joining the two steady states touches the hole in the wall before joining the other steady state (that is, in Z-space, the steady state \((1, 0)\) touches \((g_1, n_1)\), see Appendix B for details). When \( c \) is decreased below \( c = c_{\text{crit}} \) the trajectory connecting the two steady states passes through the hole in the wall before connecting to \((0, 1)\). This trajectory is no longer smooth. The hyperbolic system (with \( h_n < 0 \)) gives rise to a shock discontinuity. In particular, there is a range of wave speeds where the joining trajectory exits \((0, 1)\) and connects...
with \((1, 0)\) after jumping the wall, giving rise to a \(n\)-profile with a discontinuity, as illustrated in Fig. 2(b). The details of discontinuous solutions of the system (1) and (2) are derived in Appendix C for an arbitrary \(\chi(g) > 0\). After jumping the wall the remaining portion of the trajectory is smooth and joins the uninvaded steady state.

Alternatively, \(c_{\text{crit}}\) is defined as the value of the wave speed where the steady state \((0, 1)\) lies on the wall and therefore is a hole in the wall. When \(c\) is decreased below \(c = c_{\text{crit}}\) the two steady states are on opposite sides of the wall, then the trajectory does not pass through a hole in the wall but just jumps over the wall, in the same way as discussed above.

Defining \(n_L\) and \(n_R\) as the values of \(n\) on the left and right sides of the discontinuity respectively, an expression valid at the point of discontinuity is obtained in Appendix C as

\[
1 + \frac{\chi(g)}{c^2} \left( \frac{n_L h(g, n_L) - n_R h(g, n_R)}{n_L - n_R} \right) = 0. \tag{16}
\]

The limiting case \(n_R = 0\) corresponds to the case where \(c = c_{\text{min}}\). Then Eq. (16) reduces to
1 + \frac{\chi(1)}{c_{\text{min}}} h(1, n_L) = 0, \quad (17)

defining an equation relating \( c_{\text{min}} \) and the size of the jump. When \( c = c_{\text{min}} \) the invasion profiles have semi-compact support, as illustrated in Fig. 2(c). Therefore, discontinuous travelling wave solutions exist for a range of wave speeds \( c_{\text{min}} \leq c < c_{\text{crit}} \). When \( c < c_{\text{min}} \), no travelling wave solutions exist.

The critical feature of this discontinuity for kinetic functions (4) or (5) is that any jump in \( n \) satisfies \( W(g, n^*) = 0 \) with \( n^* = (n_L + n_R)/2 \). Therefore, the wall is located at the geometrical centre of the jump, as demonstrated in Fig. 2(b)–(c). Similar results can be obtained for more general forms of \( h \) (Appendix C).

Therefore the current existing theory provides a connection between the wave speed and the various shapes of the travelling waves which transition from smooth to discontinuous profiles. In the next sections we develop a theory regarding the shape of these smooth and discontinuous travelling wave solutions. In particular we will establish the conditions whereby the solutions are always monotone, and further develop conditions for nonmonotonicity of smooth and discontinuous travelling wave solutions.

5. Example: Generating tactically-driven nonmonotone travelling waves

To motivate our analysis, we present an example of tactically-generated travelling waves using \( \chi(g) = 1/(1 + \kappa g) \) with \( \kappa > 0 \). We use the kinetic functions (4) which do not support kinetically-generated nonmonotone solutions (Appendix A). A comparison of the solutions to this model with those in Fig. 2 for \( \chi(g) = 1 \) will demonstrate the essential requirements for the existence of nonmonotone travelling waves.

The numerical and phase plane results are given in Fig. 3 for a fixed set of parameters over a range of wave speeds. Again the continuous travelling wave profiles have been shifted so that \( n(0, t) = 0.5 \). The discontinuous travelling wave profiles have been shifted so that the discontinuity is located at \( x = 0 \). Fig. 3(a) shows a smooth invasion profile with a monotonically decreasing \( n(x, t) \) moving at speed \( c = 1 \). The corresponding phase plane shows that the trajectory does not interact with the wall. The profile in Fig. 3(b) shows a smooth nonmonotone invasion profile moving at a slower speed \( c = 0.17 \). The phase plane trajectory for this wave crosses through a hole in the wall. This trajectory intersects the \( n \)-nullcline once on either side of the wall. Fig. 3(c) shows a slower invasion profile moving at speed \( c = 0.13 \); this profile is nonmonotone and discontinuous. The phase plane trajectory crosses the \( n \)-nullcline once before jumping the wall. After jumping the wall the remaining portion of the trajectory is smooth and joins the uninvaded steady state. For this case the analysis (Appendix C) shows that the height of the leading shock is given by \( c_{\text{min}}^2/(\chi(1)(\beta + \gamma)) = 0.92 \), which is accurately predicted by the numerical algorithm.

All four travelling waves shown in Fig. 3 are different solutions to the same invasion system generated with identical parameters, except for the wave speed, yet the shape of invasion varies dramatically. Clearly there is a connection between the wave speed and the various invasion shapes which transition from (i) smooth monotone profiles, (ii) smooth nonmonotone profiles to (iii) nonmonotone discontinuous profiles as \( c \) decreases for this particular \( \chi(g) \) function. Similar transitions of shape are also generated using different \( \chi(g) \) including exponentially decreasing and polynomial forms. As illustrated in Fig. 2, equivalent computations with a constant \( \chi(g) \) for the kinetic functions (4) only give rise to monotone profiles, and therefore fail to produce the rich diversity of profile shapes.

This leads us to investigate the relationship between \( \chi(g) \), wave speed \( c \) and the shape of the travelling wave profile.

6. Analysis: Conditions necessary for a nonmonotone travelling wave

The travelling wave profile for \( n \) will be nonmonotone if the sign of \( dn/dz \) changes at least once. In the \( (g, n) \) phase plane, this corresponds to the trajectory that joins the invaded and uninvaded steady states crossing the \( n \)-nullcline \( F(g, n) = 0 \) at least once. An analysis of the slope of the \( n \)-nullcline provides a necessary condition on the existence of a smooth nonmonotone travelling wave.

Suppose the \( n \)-nullcline \( F(g, n) = 0 \) is a monotonically decreasing function of \( g \). We seek a solution where \( g(z) \) increases as \( z \) increases. This means that the trajectory joining \((0, 1)\) and \((1, 0)\) in the phase plane must always move to the right.

Suppose that the two steady states are on the same side of the wall. Then \( W > 0 \) in this region. Hence the trajectory exits \((0, 1)\) in region \( F < 0 \). (i) For smooth solutions, the trajectory must join the two steady states without any jump discontinuity. This occurs if the trajectory passes through no holes in the wall or passes through an even number of holes in the wall. It is impossible for the trajectory exiting \((0, 1)\) to intersect a monotonically decreasing \( F(g, n) = 0 \) nullcline (twice) and connect with \((1, 0)\). (ii) Suppose instead that the trajectory joining the two steady states has a jump discontinuity. Since both the nullcline and trajectory must pass through a hole in the wall, it is again impossible for the trajectory to have two crossings of the nullcline before it passes through the hole in the wall. In addition, the trajectory cannot intersect with a monotonically decreasing nullcline on the far side of the wall.

A similar argument holds if the two steady states are on opposite sides of the wall.

Therefore, if \( F(g, n) = 0 \) is a monotonically decreasing function of \( g \), the travelling wave must be monotonically decreasing function of \( z \). Accordingly, we investigate conditions when \( F(g, n) = 0 \) is not a monotonically decreasing function of \( g \).
Fig. 3. Numerical and phase plane results using (4) and $\chi(g) = 1/(1 + \kappa g)$ with $\kappa = 100, \beta = 0.1, \gamma = 1$ for various wave speeds $c$. Numerical results show $n(x,t)$ (red line), $g(x,t)$ (green line), with the discontinuity shown with two blue bullets. The phase plane shows the steady states (yellow bullets), wall $W(g, n) = 0$ (dashed line), $n$-nullcline $F(g, n) = 0$ (blue line) and the required trajectory joining the steady states (black line). Results are given with $c$ decreasing down the page: (a) $c = c^* > c^*_\text{crit}$, (b) $c^*_\text{crit} < c = 0.17 < c^*$, (c) $c^*_\text{min} < c < 0.13 < c^*_\text{crit}$ and (d) $c = c^*_\text{min} = 0.10$. The $c^*$ is defined in Section 7. All numerical simulations are performed for a sufficient time to allow the formation of the travelling wave moving with a constant speed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Eq. (12) is differentiated with respect to $g$ to give an expression for the slope of the $F(g,n) = 0$ nullcline as

$$\frac{dn}{dg} = \frac{F_g}{F_n} = -\frac{\frac{\partial^2 F}{\partial g^2}h_{gg} + \frac{\partial F}{\partial g}h_{gh} + \frac{\partial^2 F}{\partial h^2}h_{hh} - \left(\frac{\partial F}{\partial n}\right)_g}{\frac{\partial F}{\partial g}h_{gh} + \frac{\partial F}{\partial h}h_{gh} + \frac{\partial^2 F}{\partial h^2}h_{hh} - \left(\frac{\partial F}{\partial n}\right)_n}.$$

(18)

For constant $\chi(g)$ this reduces to

$$\frac{dn}{dg} = -\frac{\frac{\partial^2 F}{\partial g^2}h_{gg} + \frac{\partial F}{\partial g}h_{gh} + \frac{\partial^2 F}{\partial h^2}h_{hh} - \left(\frac{\partial F}{\partial n}\right)_g}{\frac{\partial F}{\partial g}h_{gh} + \frac{\partial F}{\partial h}h_{gh} + \frac{\partial^2 F}{\partial h^2}h_{hh} - \left(\frac{\partial F}{\partial n}\right)_n}.$$

(19)

For the kinetic functions (4) and (5), $h$ and all the partial derivatives of $f/n$ and $h$ required in (19) are nonpositive in the region of interest $0 < g < 1$. Hence for these kinetics and $\chi(g)$ constant, $F(g,n) = 0$ is a monotonically decreasing function of $g$. Therefore we have shown that such systems with constant $\chi(g)$ cannot support nonmonotone travelling waves.

Most previous phase plane analyses of the systems (8) and (9) with the kinetics (4) and (5) have focused on constant $\chi(g)$ [7,8,11,12]. Therefore, we have established a new result explaining the existence of monotone solutions and the nonexistence of nonmonotone solutions. For these kinetic functions this result also applies to any $\chi(g)$ where both $\chi'(g) \geq 0$ and $\chi''(g) \geq 0$ over $0 < g < 1$. Consequently, if a nonmonotone travelling wave solution to this particular system is numerically generated with such a $\chi(g)$, then there must be an error in the numerical algorithm. Indeed, the governing equations are nonlinear hyperbolic equations, which are susceptible to artificial oscillations introduced by standard numerical approximations [9,18].

For general kinetics with $h < 0$, if the $n$-nullcline $F(g,n) = 0$ is monotonically decreasing over $0 < g < 1$, then it is not possible for the cell density $n$ to support nonmonotone travelling waves solutions. Conversely, if a nonmonotone travelling wave is to exist, then the slope of the $n$-nullcline must be positive over some of the interval $0 < g < 1$ in order to have a crossing of the trajectory with the nullcline. Examining the expression (19) provides clues to the conditions necessary for the existence of such a positive slope. Certainly for the kinetics (4) and (5), $\chi'(g) < 0$ and/or $\chi''(g) < 0$ is required over some of the interval $0 < g < 1$, whereas if $\chi(g)$ is a constant, some of the partial derivatives of $f$ and $h$ must be sufficiently positive over some of the interval $0 < g < 1$.

7. Transition from smooth monotone to discontinuous nonmonotone travelling waves

Conditions allowing nonmonotone travelling waves to form are now investigated. From previous work described in Section 4, transitions from smooth to discontinuous solutions at $c_{\text{crit}}$ are well established. Here we establish a transition from smooth monotone to smooth nonmonotone travelling waves, followed by discontinuous nonmonotone travelling waves, as the wave speed decreases. The following arguments are developed under the assumption that the conditions for nonmonotone travelling wave solutions are met; that is, we consider only the case where the slope of the $n$-nullcline is positive over some of the interval $0 < g < 1$.

7.1. Sufficiently large wave speed: Smooth monotone invasion

For a particular $\chi(g) > 0$, we consider travelling waves over a range of $c$, starting with large $c$. In the limit as $c \to \infty$, the travelling wave system (8)–(12) relaxes to the kinetic system $dn/dg = f(g,n)/h(g,n)$ [2,20]. A trajectory joining $(0, 1)$ and $(1, 0)$ exists, and both the $n$ and $g$ profiles are monotone and continuous (since only kinetically-generated monotone solutions are considered here). This case of large $c$ corresponds to the example profile shown in Fig. 3(a). These solutions are not affected by the form of $\chi(g)$ since the flux term is not important when $c \to \infty$ [2,7].

As $c$ is reduced from $c \to \infty$, we require the $n$-nullcline to become nonmonotonic, as discussed in Section 6. For sufficiently large values of $c$, the trajectory joining $(0, 1)$ and $(1, 0)$ does not intersect this nonmonotone $n$-nullcline. Note that the $n$-nullcline in Fig. 3(a) is nonmonotone in a very small region near $(0, 1)$, but it cannot be discerned on the scale of the illustrated phase plane.

7.2. Reduced wave speed: Smooth nonmonotone invasion

As $c$ is reduced from the sufficiently large values discussed in Section 7.1, the trajectory joining $(0, 1)$ and $(1, 0)$ will intersect this nonmonotone $n$-nullcline at least twice. Hence there exists a critical wave speed $c^*$ for which the trajectory satisfies $dn/dz < 0$ for all $-\infty < z < \infty$ when $c > c^*$, but $dn/dz > 0$ for some $z$ values when $c < c^*$. Hence a smooth nonmonotone travelling wave solution develops. This transition in the $n$-profiles is shown in Fig. 3(a)–(b). It is possible that the joining trajectory can also pass through a hole in the wall as in Fig. 3(b). Such smooth nonmonotone solutions exist for a range of wave speeds $c_{\text{crit}} < c < c^*$.

7.3. Sufficiently small wave speed: Discontinuous nonmonotone invasion

As discussed in Section 4, discontinuous travelling waves exist for a range of wave speeds $c_{\text{min}} \leq c \leq c_{\text{crit}}$, for a system with kinetics $f$ and $h$ with $h_n < 0$. There is a relationship between the size of the jump and the wave speed, described by equation (16).

Several possible phase planes arise, with various relationships between the number of intersection points of the trajectory with the $n$-nullcline and the position of the wall. For all cases, the following arguments apply. Suppose a nonmonotone invasion profile for $c = c_{\text{crit}}$ has exactly two changes in sign of $dn/dz$ where the joining trajectory crosses $F(g,n) = 0$. When $c_{\text{min}} < c < c_{\text{crit}}$, part of the invasion profile is removed by a discontinuity in $n$. Depending on the kinetics, the discontinuity can occur in the monotonically decreasing leading edge of $n$, or it can be located further behind the front face where $n$ is monotonically increasing. The details of the shape of $n$ to the left of the discontinuity are explored in full for the minimum wave speed case $c = c_{\text{min}}$. After the discontinuity, the toe of the $n$-profile monotonically decreases to zero.
7.4. Minimum wave speed: Discontinuous nonmonotone invasion

The existence of a travelling wave with semi-compact support corresponding to $c_{\text{min}}$ for a system with kinetics $f$ and $h$ with $h_0 < 0$ has been well established, as discussed in Section 4. However, these results say nothing about the monotonicity or otherwise of the solutions. Here we establish a necessary and sufficient condition for such semi-compact support travelling waves to be nonmonotone.

If the joining trajectory crosses the $F(g, n) = 0$ nullcline an odd number of times (excluding crossings at holes in the wall), a necessary and sufficient condition can be established for nonmonotone travelling waves.

**Theorem.** Consider the system (1) and (2) with two steady states $(0, 1)$ and $(1, 0)$ where $h_0 < 0$ and $c = c_{\text{min}}$. The travelling wave solution for $n$ is nonmonotone with an odd number of turning points if and only if $F(1, n_L) < 0$.

**Proof.** We must consider two cases: one where the steady states are on the same side of the wall (Fig. 4(a)), and one where they are not (Fig. 4(b)). Note that $(1, 0)$ always lies where $W > 0$.

(i) Suppose the steady states are on the same side of the wall ($W > 0$). The trajectory from $(0, 1)$ starts below both the wall and $n$-nullcline where $W(0, 1) > 0$ and $F(0, 1) < 0$ giving $dn/dz < 0$ (Fig. 4(a)). For $c = c_{\text{min}}$ the trajectory must jump the wall to connect with $(1, 0)$. Hence, the trajectory must pass through a hole in the wall and move into the region where $W(g, n) < 0$. Since $dn/dz$ is continuous at the hole in the wall, the sign of $F$ must switch as the trajectory passes through the hole in the wall. Consider the value of $F$ at the point $(1, n_L)$ where the trajectory jumps to $(1, 0)$. Hence, $F(1, n_L) < 0$ is a necessary and sufficient condition for the trajectory to cross the $n$-nullcline an odd number of times. Note that if $F(1, n_L) > 0$, then the trajectory may not have crossed the $n$-nullcline, giving a monotone profile, or it may have crossed it an even number of times, giving a profile with an even number of turning points.

(ii) Now suppose the steady states are on opposite sides of the wall. For this case, the trajectory starts where $W(0, 1) < 0$ and $F(0, 1) > 0$ giving $dn/dz < 0$ (Fig. 4(b)). The trajectory must jump the wall to connect with $(1, 0)$ at $c = c_{\text{min}}$. Hence $F(1, n_L) < 0$ is a necessary and sufficient condition for the trajectory to cross the $n$-nullcline an odd number of times. Again if $F(1, n_L) > 0$, then the trajectory may not have crossed the $n$-nullcline, giving a monotone profile, or it may have crossed it an even number of times, giving a profile with an even number of turning points.

This theorem applies to solutions where the $n$-profile is monotonically increasing to the left of the discontinuity. The theorem cannot apply to those solutions where the $n$-profile is nonmonotone but decreasing immediately behind the discontinuity. For these cases, there are an even number of turning points and $F(1, n_L) > 0$. The commonly studied monotone profiles with no turning points also satisfy $F(1, n_L) > 0$. No equivalent existence theorem can be established for the case of an even number of turning points. However, clearly the trajectory must cross $F = 0$ an even number of times (excluding crossings at holes in the wall).

Example numerical profiles and trajectories with an odd and even number of turning points are given in Fig. 5. In both cases the steady states are on the same side of the wall. In Fig. 5(a), the trajectory passes through the hole in the wall and then intersects $F(g, n) = 0$ once above the wall. The jump occurs with $n_L$ below the $n$-nullcline and above the wall so that $F(1, n_L) < 0$ and $dn/dz > 0$ immediately before the jump. This corresponds to the $n$-profile having a positive slope immediately behind the leading shock. In Fig. 5(b), the trajectory intersects $F(g, n) = 0$ twice below the wall and then passes through a hole in the wall. The jump occurs with $n_L$ above both the $n$-nullcline ($F(1, n_L) > 0$) and the wall so that $dn/dz < 0$ just before the jump. This corresponds to the $n$-profile having a negative slope immediately behind the leading shock. Therefore the theorem applies to Fig. 5(a) but not to Fig. 5(b).

Although this theorem is developed for $c = c_{\text{min}}$, we expect, by continuity, that a system satisfying $F(1, n_L) < 0$ at $c = c_{\text{min}}$ also supports a discontinuous nonmonotone travelling wave with a smooth leading edge (demonstrated previously in Fig. 3(c)) for some larger values of the wave speed. In this
case the solution will be discontinuous but does not have semi-compact support.

7.5. Summary

Table 1 summarizes the possible transitions and characteristics of various travelling wave profiles possible for the system (1) and (2) as a function of wave speed $c$. The values of $c^*$, $c_{\text{crit}}$ and $c_{\text{min}}$ can be determined numerically. The transition from smooth or discontinuous travelling waves at $c = c_{\text{crit}}$, as well as the minimum wave speed $c = c_{\text{min}}$, has been well established. Here we have introduced a new transition value $c^*$ that defines the transition from smooth monotone to smooth non-monotone travelling waves. Table 1 summarizes how the new results obtained here relate to previous results.

The existence of smooth monotone travelling waves for fast invasion with $c > c^*$ is a consequence of previous arguments for diffusive migration [2] applied to tactic migration. The existence of nonmonotone discontinuous solutions with semi-compact support have been analysed in this work for the first time. Our new results developed here will enable us to show that certain previously documented nonmonotone profiles ought to be monotone and the cause of the nonmonotone shapes is due to numerical error. The existence of nonmonotone discontinuous profiles without semi-compact support and nonmonotone smooth profiles are demonstrated here, both numerically and analytically in the phase plane. However it is only for the most important speed $c = c_{\text{min}}$ that the analysis leads to the condition $F(1, n_L) < 0$.

The transitions described in Table 1 have been proved (using hyperbolic partial differential equation theory and phase plane arguments) and demonstrated numerically in Fig. 3. However, it is not possible to exactly determine the invasion speeds at which these transitions occur for a general tactic invasion problem a priori. This is because the exact values of $c_{\text{min}}$, $c_{\text{crit}}$ and $c^*$ cannot be analytically deduced; we must rely on numerical experimentation to demonstrate and quantify the speeds at which these transitions occur.

When numerical simulations are used to determine whether a particular form of $\chi(g)$ can support nonmonotone travelling wave solutions, it is best to focus on the minimum wave speed solution. This approach is more efficient than looking at solutions with larger wavespeeds since the invasion profiles for sufficiently large $c$ can look very similar regardless of whether or not $\chi(g)$ supports a nonmonotone solution for slower speeds or not.

8. Applications

The theoretical results developed here are applied to three cases of tactic invasion. First, we consider the general case of constant $\chi(g)$ and survey how our analysis applies to previously
Table 1
Summary of possible transitions from smooth monotone travelling wave invasion profiles to discontinuous nonmonotone travelling wave invasion profiles over a range of wave speeds $c$ for a system (1) and (2) where $h < 0$ and $h_n < 0$

<table>
<thead>
<tr>
<th>Wave speed $c$</th>
<th>Travelling wave shape</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c &gt; c^*$</td>
<td>Monotone and smooth</td>
<td>Previously demonstrated and analysed [8,11,12,15].</td>
</tr>
<tr>
<td>$c_{\text{crit}} &lt; c &lt; c^*$</td>
<td>Smooth</td>
<td>Existence of nonmonotone profiles analysed here.</td>
</tr>
<tr>
<td>$c_{\text{min}} &lt; c &lt; c_{\text{crit}}$</td>
<td>Discontinuous</td>
<td>Existence of nonmonotone profiles analysed here.</td>
</tr>
<tr>
<td>$c = c_{\text{min}}$</td>
<td>Discontinuous</td>
<td>Necessary and sufficient condition for an odd number of turning points given here.</td>
</tr>
<tr>
<td>$0 &lt; c &lt; c_{\text{min}}$</td>
<td>With semi-compact support</td>
<td>Certain previous profiles with $\chi(g) = 1$ are incorrect due to numerical error [7,15]. Others are correct [13,21].</td>
</tr>
<tr>
<td></td>
<td>No travelling wave solution</td>
<td>Previously demonstrated and analysed [8,11,12,15].</td>
</tr>
</tbody>
</table>

documented results. Second we analyse two specific cases of tactic invasion with different $\chi(g)$ functions: (i) we revisit the example demonstrated in Fig. 3 and (ii) we analyse the example considered recently by Marchant et al. [13].

8.1. Example 1: Previous results with constant $\chi(g)$

As previously stated in Section 6, tactic invasion models with kinetic functions (4) or (5) with constant $\chi(g)$ do not support nonmonotone travelling waves. Therefore nonmonotone travelling wave profiles documented in the literature under these conditions are erroneous. For example, Perumpanani et al. [15] acknowledge that the discontinuous nonmonotone travelling wave profiles in their manuscript (p. 154, Figure 6A) are subject to numerical error since their numerical results are grid dependent. Similarly, Landman et al. [7] numerically solved a chemotaxis-dominant invasion model with constant $\chi(g)$ and observed the formation of nonmonotone invasion waves. The profiles with larger $\chi$ values are also subject to numerical error since our analysis shows that nonmonotone profiles do not exist under these circumstances. These two examples serve to illustrate that extreme care should be exercised when using standard numerical approximations for nonlinear hyperbolic conservation laws.

8.2. Example 2: Kinetic functions (4) and $\chi(g) = 1/(1 + \kappa g)$

For $c = c_{\text{min}}$ with the kinetics (4), the height of the leading shock is $n_L = c_{\text{min}}^2/\{\chi(1)/(\beta + \gamma)\}$ (Appendix C). The condition $F(1, n_L) < 0$ for a nonmonotone travelling wave moving at $c_{\text{min}}$ is given by

$$c_{\text{min}}^2 \left[ \frac{1 + \gamma}{\beta + \gamma} + \frac{\chi'(1)}{\chi(1)} \right] < 1 - \beta.$$  \hspace{1cm} (20)

For $\chi(g) = 1/(1 + \kappa g)$, (20) reduces to

$$c_{\text{min}}^2 \left[ 1 + (1 + \kappa) \frac{1 - \beta}{\beta + \gamma} \right] < 1 - \beta.$$  \hspace{1cm} (21)

This condition has several important consequences. If $\beta = 1$, then (21) is never satisfied. If $\beta < 1$, numerical experimentation revealed that (21) can be satisfied with sufficiently large $\kappa$. For the results shown in Fig. 3 with $\kappa = 100$ and $c_{\text{min}} = 0.1$, the condition (21) is satisfied, giving rise to a shock-fronted solution which has a increasing region immediately behind the shock. For $\beta > 1$, we were unable to find a particular combination of parameters and $c_{\text{min}}$ that satisfied (21). It is not possible to predict which parameters satisfy (21) a priori as the dependence of $c_{\text{min}}$ on the parameters $\beta$, $\gamma$ and $\kappa$ is unknown [8].

Further numerical simulations for the same kinetic parameters as in Fig. 3 shows that (21) fails to hold for some critical value of $\kappa$ as $\kappa$ is decreased. Numerical experimentation shows that minimum wave speed simulations with $\kappa \geq 2$ are nonmonotone while simulations with $\kappa \leq 1$ are monotonically decreasing and shock fronted.

8.3. Example 3: Kinetic functions (5) and $\chi(g) = g^4/(1 + g^5)^2$

We apply our results to the haptotaxis invasion results recently published by Marchant et al. [13], using kinetic functions (5). Marchant et al. considered a concave down haptotactic sensitivity function given by $\chi(g) = g^4/(1 + g^5)^2$ and initial conditions $\hat{g}(x, t) = \hat{g}$ on $0 < x < L$ and $\hat{g} = 1.25$. This problem can be rescaled to our system by choosing $\chi(g/\hat{g})$ and $\hat{g} = 1$ as the initial condition.

The condition $F(1, n_L) < 0$ with $n_L = c_{\text{min}}^2/\chi(1)$ and (5) reduces to

$$\frac{c_{\text{min}}^2}{\chi(1)} \left[ 3 \chi(1) + \chi'(1) \right] - 1 < 0.$$  \hspace{1cm} (22)

If $\chi'(1)$ is sufficiently negative then (22) may be satisfied giving rise to a nonmonotone and shock-fronted travelling wave. Our numerical simulations of Marchant’s problem (Figure 16 in [13]) after rescaling shows that $c_{\text{min}} = 0.38$. This value satisfies (22). This is consistent with the nonmonotone travelling wave profile observed by Marchant [13]. Our analysis shows that the formation of nonmonotone travelling waves depends critically on the choice of $\hat{g}$. For this $\chi(g)$ function, there exists a $\hat{g}_{\text{crit}}$ where $\hat{g} < \hat{g}_{\text{crit}}$ supports only monotonically decreasing shock-fronted invasion waves while $\hat{g} > \hat{g}_{\text{crit}}$ gives rise to nonmonotone shock-fronted invasion waves. Numerical experimentation suggests that $\hat{g}_{\text{crit}} \simeq 0.97$. Finally, further numerical simulations also confirmed that Marchant’s problem permits nonmonotone travelling waves with other $\chi(g)$ functions such as exponentially decreasing forms.
9. Conclusions

We have demonstrated that a tactic cell flux term can generate a nonmonotone cell density travelling wave. In addition, our analysis shows that tactic models of cell invasion can support a wide range of cell density profiles including (i) smooth monotone, (ii) smooth nonmonotone, (iii) discontinuous nonmonotone and (iv) discontinuous nonmonotone profiles with semicom pact support. The transition from one profile to the other is determined by the speed of invasion. Theoretical results for the existence of travelling waves that exhibit a nonmonotone region behind a jump discontinuity have been established. Only monotone solutions exist if the $n$-nullcline is monotonically decreasing over the range of $g$ (here $0 < g < 1$). If the $n$-nullcline has a turning point, then nonmonotone solutions are possible. At the minimum wave speed $c_{\text{min}}$, a necessary and sufficient condition for an increasing region to lie immediately behind the leading shock has been developed. The trajectory in the phase plane must lie below the $n$-nullcline, and this translates to an inequality involving the kinetic parameters, $c_{\text{min}}$ and $\chi$ and $\chi'$ evaluated at the uninvaded $g$ value (here $g = 1$).

This analysis explains why most previous results have simple monotone shapes when $\chi(g)$ is constant. For those cases where $\chi(g)$ is a monotonically decreasing function, $\chi'(1)$ must be sufficiently negative in order to support a nonmonotone travelling wave. Since decreasing forms of $\chi(g)$ are biologically relevant [1,14,22], we expect that such nonmonotone travelling waves have practical significance. Furthermore, our analysis explains the existence of the nonmonotone profile recently published by Marchant et al. [13]. It is worth noting that considerably more complex invasion profiles are possible. For example, profiles with multiple nonmonotone regions and multiple discontinuities can be generated with $\chi(g) = 2 + \sin(4\pi g)$ and other oscillatory functions [21].

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Appendix A. Stability of the steady states and the kinetic model

Here we describe the dynamics of the purely kinetic model, where $t$ is the independent variable. In the phase plane we require a trajectory $(g(t), n(t))$ joining $(0, 0)$ to $(0, 1)$ as $t$ increases from $-\infty$ to $\infty$. Hence $(0, 0)$ must be either a saddle or an unstable node (given that $n \geq 0$ is required), while $(0, 1)$ must be either a saddle, stable node or stable spiral. Furthermore we require $\lambda > 0$ and $\Delta < 0$ locally near $(0, 0)$ so that $n$ increases from zero, while $g$ decreases from 1.

The approach to $(0, 1)$ as $t \to \infty$ must be through the eigenvalue with negative real part. For the sake of argument here, we assume that the eigenvalue is real, and call it $-\lambda_\ast$, where $\lambda_\ast > 0$. Then, the associated eigenvector determines that the slope of the trajectory at $(0, 1)$ is $-f_g/(\lambda_\ast + f_n)$. The slope of the $n$-nullcline is $-f_g/f_n$.

By considering the relationship between the slope of the $n$-nullcline and the trajectory entering $(0, 1)$, several $(g, n)$ phase planes are possible; some of these are illustrated in Fig. 6. Fig. 6(a), (b) and (d) support monotonically increasing $n(t)$ and decreasing $g(t)$ as $t$ increases. Fig. 6(c) and (e) support a $n(t)$, which is initially monotonically increasing but overshoots the steady value for some $t$ and then decreases to the steady state. For this case, the trajectory crosses the $n$-nullcline. We describe
this second case, illustrated in Fig. 6(c) and (e), as a kinetically-generated nonmonotone solution, while in the other three cases there is no such kinetically-generated nonmonotone solution.

If one of the steady states is a saddle then there is a unique trajectory joining the steady states. This is the case for kinetic functions (4) and (5), where (1, 0) is a saddle. On the other hand if both steady states are nodes or spirals, then there are multiple solutions.

The kinetic functions (4) and (5) do not produce kinetically-generated nonmonotone solutions. However, a kinetically-generated nonmonotone solution is produced by the kinetic functions used in Fig. 1 with \( \delta > 0 \).

If the reaction terms in the invasion model support a kinetically-generated nonmonotone solution, then the introduction of a cell flux term preserves the nonmonotonicity and the travelling wave cell density \( n \) profile will be nonmonotone under certain conditions due to the kinetics. In particular, if there is a flux (for example, a diffusive or chemotactic flux), then the perturbation solution of Canosa [2] establishes that the first order approximation to the shape of the travelling wave solution is given by the kinetic terms. If there is no kinetically-generated nonmonotone solution, then a diffusive flux cannot generate a nonmonotone travelling wave.

**Appendix B. Phase plane trajectory through a hole in the wall**

The nature of the hole in the wall, \((g_h, n_h)\), is determined by considering properties of the Jacobian \( K \) in (15). The \( \text{Det}(K) \) can be written as

\[
\text{Det}(K) = H F_N W_N S,
\]

where

\[
S = \left( -\frac{F_G}{F_N} - \frac{W_G}{W_N} \right),
\]

evaluated at \((g_h, n_h)\). The quantity \( S \) is the difference between the slope of the \( F(g, n) = 0 \) nullcline and slope of the wall \( W(g, n) = 0 \).

Schematic diagrams of possible phase planes allow us to determine the sign of \( \text{Det}(K) \). The sign of \( F_N \) and \( W_N \) are determined by holding \( N = n_h \) and increasing \( G \). For example, in Fig. 7(a) \( F_N > 0 \), while \( W_N < 0 \), and \( S > 0 \). Then \( \text{Det}(K) < 0 \), so the hole is a saddle in \( Z \)-space. Therefore, there is one direction along which two trajectories enter the hole. In \( Z \)-space this transforms to one trajectory passing through the hole in the wall at a finite \( z \). Hence, it is possible to have a trajectory leaving \((0, 1)\) as \( z \to \infty \) and passing through the hole in the wall. A second example, in Fig. 7(b), again has \( F_N > 0 \) and \( W_N < 0 \), but now \( S < 0 \) giving \( \text{Det}(K) > 0 \). Therefore the hole is a node or spiral in \( Z \)-space. It is necessary for it to be an unstable node in \( Z \)-space so that all trajectories leave \((g_h, n_h)\). Returning to \( Z \)-space, the direction of the trajectories on the top side of the wall, where \( W < 0 \), are then reversed, giving an infinite number of trajectories entering the hole from above the wall and leaving the hole below the wall.

**Appendix C. Conditions for discontinuous solutions**

The existence of discontinuous travelling wave solutions are determined using the Lax entropy condition and the Rankine–Hugoniot jump condition [3].

Writing (1) and (2) in conservation form as \( \partial P/\partial t + \partial Q/\partial x = S \) and defining \( u = \partial g/\partial x \) we identify

\[
P = \begin{bmatrix} g \\ u \\ n \end{bmatrix}, \quad Q = \begin{bmatrix} 0 \\ -h \\ \chi nu \end{bmatrix}, \quad S = \begin{bmatrix} h \\ 0 \end{bmatrix}.
\]

(24)

This first order system has characteristic slopes determined by the eigenvalues of \( \partial Q/\partial P \). For \( n > 0 \), the two nonzero eigenvalues are \( \lambda_{\pm} = -\frac{1}{2} \left[ \chi u \pm \sqrt{\chi^2 u^2 - 4n\chi h_n} \right] \). If the eigenvalues are real and distinct, that is if \( \chi^2 u^2 - 4n\chi h_n > 0 \), then the system is strictly hyperbolic. For kinetic functions with \( h_n < 0 \) (such as (4) or (5)) this condition is satisfied.

For any discontinuity moving at speed \( c \), the Rankine–Hugoniot jump condition [3] requires \([P]c = [Q]\) where \([g]\) denotes the jump in the quantity \( g \). For our system, \( g \) is continuous while \( n \) and \( u \) may have a discontinuity. Using the definition \( u = \partial g/\partial x = -h/c \), the jump conditions are

\[
[n]c = [n\chi u] = \left[ -\frac{1}{c} n\chi h \right], \quad [u]c = [-h].
\]

(25)

Using the definition \([n] = n_L - n_R\), where \( n_L \) and \( n_R \) are the values of \( n \) on the left and right side of the discontinuity respectively, we can write

\[
1 + \frac{\chi(g)}{c^2} \left( \frac{n_L h(g, n_L) - n_R h(g, n_R)}{n_L - n_R} \right) = 0.
\]

(26)
A discontinuity is possible provided \( n_R \geq 0 \) and the limiting case of \( n_R = 0 \) corresponds to the case where \( c = c_{\text{min}} \). For right travelling waves the Lax entropy condition is satisfied only if \( n_L > n_R \) [3].

For the minimum wave speed case with \( n_R = 0 \), (26) reduces to

\[
1 + \frac{\chi(1)}{c_{\text{min}}} h(1, n_L) = 0, \tag{27}
\]

defining an equation relating \( c_{\text{min}} \) and the size of the jump. It follows that \( W(1, n_L) < 0 \) using (11), (27) and our assumption that \( h_n < 0 \). Hence the point \((1, n_L)\) lies above the wall.

For a general kinetic function \( h \) with the form

\[
h(g, n) = -n^m U(g) + V(g), \tag{28}
\]

where \( m \) is a positive integer and \( U \) and \( V \) are continuous functions, a relationship between the wall and the length of the jump is obtained, as

\[
W(g, n^*) = 0, \quad \text{where } n^* = \left[ \frac{\sum_{k=0}^{m} n_L^{m-k} n_R^k}{m+1} \right]^{1/m}. \tag{29}
\]

When \( m = 1 \) as in (4) and (5), \( n^* \) is the geometrical centre of the jump [8,12]. For the minimum wave speed solution \((n_R = 0)\), (29) reduces to \( n^* = n_L/(m+1)^{1/m} \).

References