# Expanding Populations Supplementary Information

Daniel Swartz, Hyunseok Lee, Mehran Kardar, and Kirill Korolev

December 2022

## 1 Perturbative treatment of pushed waves

Here we explain in detail how to perform the perturbative treatment in the pushed wave case introduced in the main text. The starting point is the coupled FKPP and KPZ equations

$$\frac{\partial f}{\partial t} = s_0(f - f_0)f(1 - f) + D_f\frac{\partial^2 f}{\partial x^2} + v_0\frac{\partial f}{\partial x}\frac{\partial h}{\partial x} \tag{1}$$

$$\frac{\partial h}{\partial t} = v_0 + \alpha f + D_h\frac{\partial^2 h}{\partial x^2} + \frac{v_0}{2}\Big(\frac{\partial h}{\partial x}\Big)^2. \tag{2}$$

We can remove the first term in Eq. (2) by shifting to a comoving frame and making the substitution $h \to h + v_0 t$. In this comoving frame, we are interested in travelling wave solutions which are fully described in a comoving coordinate $z = x - ut$ which moves with a speed $u$ to be determined. For travelling wave solutions, Eqs. (1) and (2) take the form

$$-uf'(z) = s_0(f - f_0)f(1 - f) + D_f f''(z) + v_0 f'(z)h'(z) \tag{3}$$

$$-uh'(z) = \alpha f(z) + D_h h''(z) + \frac{v_0}{2}h'(z)^2 \tag{4}$$

Further, we will consider the initial conditions $h(x, t = 0) = 0$ and $f(x, t = 0) = \theta(-x)$, corresponding to a half-space where the region $x < 0$ is occupied by mutant and $x > 0$ is occupied by wildtype. We will also analyze traveling waves for which the height field attains a constant slope $\sigma$ as the mutant propagates into the wildtype. Eq. (4) immediately implies

$$-u\sigma = \alpha + \frac{v_0}{2}\sigma^2\,, \tag{5}$$

where we have used the fact $f \approx 1$ in region occupied by mutant. Eq. (5) provides a key relation between $u$ and $\alpha$ and is exact.

We shall treat the nonlinear coupling $v_0 f'(z)h'(z)$ in Eq. (3) as as a perturbation. In the absence of this term, the solution for $f(z)$ is

$$f^{(0)}(z) = \frac{1}{1 + e^{z/a}}\,, \tag{6}$$

where $a = \sqrt{\frac{2D_f}{s_0}}$ and the uncoupled velocity is $u_0 = \sqrt{\frac{s_0 D_f}{2}}(1 - 2f_0)$.Substituting this zeroth order result in Eq. (4) leads to

$$-uh^{(1)\prime}(z) = \alpha\frac{1}{1 + e^{z/a}} + D_h h^{(1)\prime\prime}(z) + \frac{v_0}{2}h^{(1)\prime}(z)^2\,. \tag{7}$$

Substituting the resulting $h^{(1)}$ into Eq. (3) leads to

$$-uf^{(1)\prime}(z) = s_0(f^{(1)} - f_0)f^{(1)}(1 - f^{(1)}) + D_f f^{(1)\prime\prime}(z) + v_0 f^{(1)\prime}(z)h^{(1)\prime}(z)\,. \tag{8}$$

Following the approach discussed in [4, 6, 5, 7], we expand the terms in Eq. (8) as $f^{(1)} = f^{(0)} + \delta f$ and $u = u_0 + \delta u$ and neglect terms of order $O(\delta f^2, \delta u^2, \delta f\delta u)$. We will further neglect terms like $h^{(1)\prime}\delta f'$, which are second order in a perturbation is $h^{(1)\prime}$, corresponding to small slope.

$$-\delta u f^{(0)\prime} - v_0 f^{(0)\prime}h^{(1)\prime} = u_0\delta f' + s_0\frac{\partial}{\partial f}\Big[(f - f_0)f(1 - f)\Big]\Big|_{f=f^{(0)}}\delta f + D_f\delta f'' = \mathcal{L}\delta f.$$

The RHS involves a linear operator $\mathcal{L}$ which has a left eigenvector $L(z)$ with eigenvalue zero (that is, $\mathcal{L}^\dagger L(z) = 0$). The eigenvector $L(z)$ is

$$L(z) = e^{u_0 z/D_f} f^{(0)\prime}. \tag{9}$$

Multiplying both sides of our expanded Eq. (3) by $L(z)$ and integrating over all $z$, the RHS vanishes by the eigenvector property of $L$, and we find a closed form expression for the correction to the invasion velocity

$$\delta u = -v_0 \frac{\int_{-\infty}^{\infty} (f^{(0)\prime})^2 e^{u_0 z/D_f} h^{(1)\prime} dz}{\int_{-\infty}^{\infty} (f^{(0)\prime})^2 e^{u_0 z/D_f} dz}. \tag{10}$$

Given a result for $h^{(1)}$, as discussed next, the ratio of integrals can be evaluated numerically to give the numerical value of $\kappa$.

# 2 The Cole-Hopf transformation

Eq. (7) can be solved exactly with the use of a Cole-Hopf transformation, $w \equiv \exp\left[(v_0 h/(2D_h)\right]$, where we substitute $h^{(1)\prime}(z) = \frac{2D_h}{v_0} w'(z)/w(z)$. Equation (7) then simplifies to

$$w'' + \frac{u}{D_h} w' + \frac{1}{1+e^{z/a}} \frac{\alpha v_0}{2D_h^2} w = 0\,. \tag{11}$$

This simplified equation has two solutions $w_1$ and $w_2$ given by

$$\begin{aligned} w_1 &= e^{-\frac{u+\sqrt{u^2-2\alpha v_0}}{2D_h} z}\, {}_2F_1\Big(-\frac{u+\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, \frac{u-\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, 1-2\frac{\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, -e^{z/a}\Big)\,, \\ w_2 &= e^{\frac{u-\sqrt{u^2-2\alpha v_0}}{2D_h} z}\, {}_2F_1\Big(-\frac{u-\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, \frac{u+\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, 1+2\frac{\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, -e^{z/a}\Big)\,, \end{aligned}$$

where ${}_2F_1$ is a hypergeometric function. The general solution to Eq. (11) is then a linear combination of $w_1$ and $w_2$. When mapping these solutions back onto the height field $h$, only $w_2$ satisfies the essential boundary condition that $h^{(1)\prime} \to 0$ as $\alpha \to 0$. This is most immediately seen using the fact that the ${}_2F_1$ function is unity when its first argument vanishes. For this reason we throw out $w_1$. The slope of the height field is then

$$\begin{aligned} h^{(1)\prime} =& \frac{-u+\sqrt{u^2-2\alpha v_0}}{v_0} \\ &+ e^{z/a} \frac{\alpha v_0^2 a/D_h}{1+a\sqrt{u^2-2\alpha v_0}/D_h} \frac{{}_2F_1(1-\frac{u-\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, 1+\frac{u+\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, 2+2\frac{\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, -e^{z/a})}{{}_2F_1(-\frac{u-\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, \frac{u+\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, 1+2\frac{\sqrt{u^2-2\alpha v_0}}{2D_h a^{-1}}, -e^{z/a})}\quad . \end{aligned} \tag{12}$$

The expression for $h^{(1)\prime}$ is formally exact, and can be substituted into Eq. (10) to give a nonlinear equation for $u$ which can then be solved numerically. This is a complex numerical task which can be circumvented in the limit $\alpha \to 0$ which is identified with a small slope expansion.

## 2.1 Linear approximation for small $\alpha$

For small $\alpha$, a direct expansion of Eq. (12) yields a simplified form of $h^{(1)\prime}$,

$$h^{(1)\prime}(z) = -\frac{\alpha}{u}\, {}_2F_1\left(1, \frac{au}{D_h}, 1+\frac{au}{D_h}, -e^{z/a}) + O(\alpha^2)\right). \tag{13}$$

This expression is also obtainable by solving Eq. (7) while ignoring the quadratic term, which is anticipated to be $O(\alpha^2)$. Following the methodology of the expansion of Eq. (8), we decompose $u = u_0 + \delta u$. As the original equations are decoupled for $\alpha = 0$, $\delta u$ must be $O(\alpha)$ and thus can be neglected in Eq. (13). The

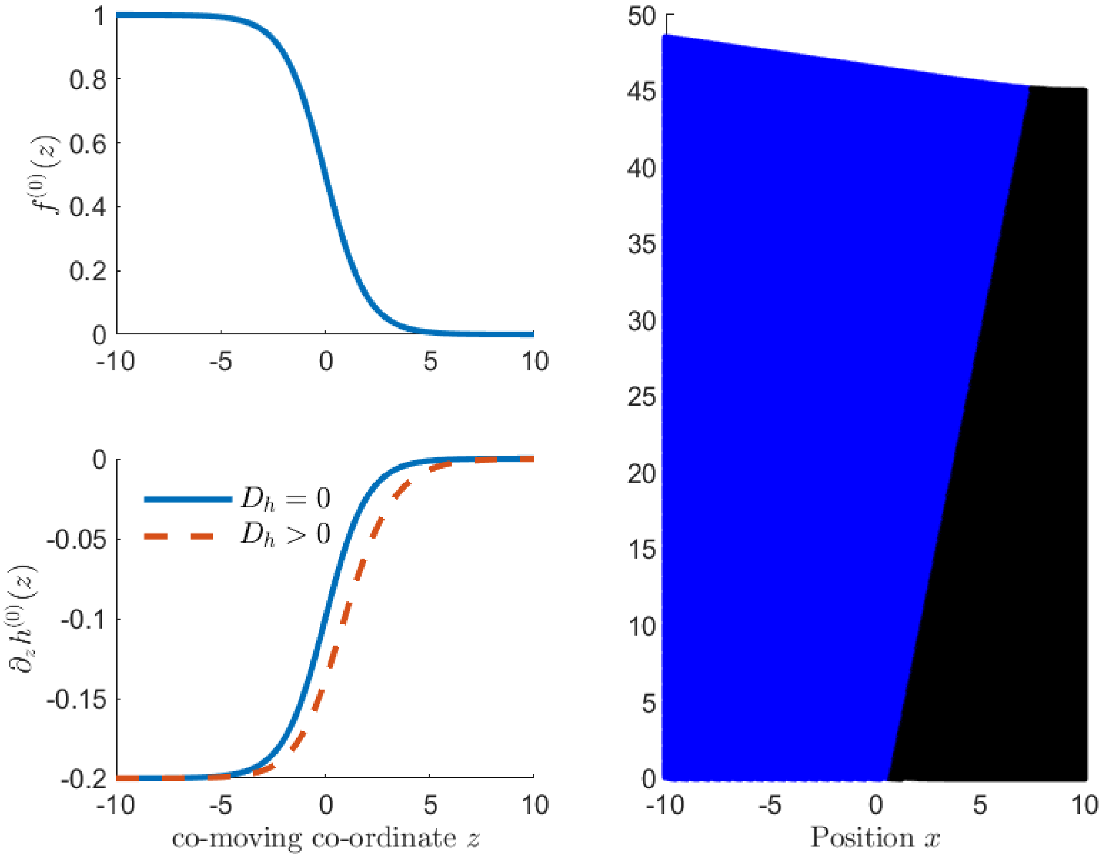


Figure 1: Sample showing the solution to the travelling wave problem in the geometric limit. (Top Left) Plot showing the zeroth order mutant frequency wave form (6) as a function of the co-moving co-ordinate $z = x - ut$. (Bottom Left) The solid line is the solution to Eq. (7) in the geometric limit and for small $\alpha$ from Eq. (16). The dashed line is the solution with surface relaxation, again in the small $\alpha$ limit, as given by Eq. (13). The right plot is the morphology generated in the geometric limit. The height field is found by integrating Eq. (16). This surface expands along its unit normal, and the speed of invasion is given by Eq. (17).

approximate form of $h^{(1)\prime}$ is then further simplified with the use of Eq. (5) to replace $\alpha$ with $\sigma$ (to leading order). The final expression for $h^{(1)\prime}$ is

$$h^{(1)\prime}(z) \approx \sigma \;{}_2F_1\left(1, \frac{au_0}{D_h}, 1 + \frac{au_0}{D_h}, -e^{z/a}\right). \tag{14}$$

This can now be immediately substituted into Eq. (10), and the integrals can be calculated numerically to give a closed-form solution for the correction to the invasion veloctiy $\delta u$. This is the method used to calculate the theoretical values of $\kappa$ reported in Figs. (3) and (4) in the main text.

## 2.2 The geometric limit

A further limit can be taken, which provides the advantage of simplifying the result of integrating Eq. (10). We call this limit the "geometric limit" which is achieved by setting $D_h = 0$. Physically, the geometric limit corresponds to the case where the height field $h$ no longer relaxes due to surface rearrangement and instead only advances along the direction of the unit normal. The geometric limit also corresponds to the "equal time" approach discussed in previous works [3, 2]. Such a limit allows for the case of cusps and sharp corners, in the height field. It is simplest to proceed from Eq. (7), with $D_h = 0$. The resulting quadratic equation is readily solved to give

$$h^{(1)\prime}(z) = \frac{-u \pm \sqrt{u^2 - 2\alpha v_0 f^{(0)}(z)}}{v_0}. \tag{15}$$

Upon substitution into Eq. (10), we again encountered a nonlinear equation for $u$. We further simplify it again expanding in small $\alpha$, where the height profile is now

$$h^{(1)\prime}(z) \approx \sigma f^{(0)}(z). \tag{16}$$

We have again used Eq. (5) to remove $\alpha$. Eq. (10) can now be integrated exactly, and we find

$$\delta u = -v_0\Big(\frac{1}{4} + \frac{f_0}{2}\Big)\sigma, \tag{17}$$

a rather simple expression for the correction to the invasion velocity.

The $D_h = 0$ limit is singular, and leads to jagged profiles that are smoothed for $D_h > 0$. However this form of $\kappa$ makes explicitly clear that the correction to the wave-speed should vanish as $f_0 \to -1/2$. This value of $f_0$ is known to correspond with the onset of pulled waves [1, 8]. This feature is general, the $D_h > 0$ correction also vanishes for $f_0 \to -1/2$ which can be verified by showing the denominator of Eq. (10) diverges while the numerator remains finite.

# References


[1] Gabriel Birzu, Oskar Hallatschek, and Kirill S Korolev. Fluctuations uncover a distinct class of traveling waves. *Proceedings of the National Academy of Sciences*, 115(16):E3645–E3654, 2018.

[2] Oskar Hallatschek and David R Nelson. Life at the front of an expanding population. *Evolution: International Journal of Organic Evolution*, 64(1):193–206, 2010.

[3] Kirill S Korolev, Melanie JI Müller, Nilay Karahan, Andrew W Murray, Oskar Hallatschek, and David R Nelson. Selective sweeps in growing microbial colonies. *Physical biology*, 9(2):026008, 2012.

[4] Baruch Meerson, Pavel V Sasorov, and Yitzhak Kaplan. Velocity fluctuations of population fronts propagating into metastable states. *Physical Review E*, 84(1):011147, 2011.

[5] AS Mikhailov, L Schimansky-Geier, and W Ebeling. Stochastic motion of the propagating front in bistable media. *Physics Letters A*, 96(9):453–456, 1983.

[6] GC Paquette, Lin-Yuan Chen, Nigel Goldenfeld, and Y Oono. Structural stability and renormalization group for propagating fronts. *Physical review letters*, 72(1):76, 1994.

[7] Andrea Rocco, Jaume Casademunt, Ute Ebert, and Wim van Saarloos. Diffusion coefficient of propagating fronts with multiplicative noise. *Physical Review E*, 65(1):012102, 2001.

[8] Wim Van Saarloos. Front propagation into unstable states. *Physics reports*, 386(2-6):29–222, 2003.