



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

## Speed of Invasion of an Expanding Population by a Horizontally Transmitted Trait

**Citation for published version:**

Venegas-Ortiz, J, Allen, RJ & Evans, MR 2014, 'Speed of Invasion of an Expanding Population by a Horizontally Transmitted Trait', *Genetics*, vol. 196, no. 2, pp. 497-+.  
<https://doi.org/10.1534/genetics.113.158642>

**Digital Object Identifier (DOI):**

[10.1534/genetics.113.158642](https://doi.org/10.1534/genetics.113.158642)

**Link:**

[Link to publication record in Edinburgh Research Explorer](#)

**Published In:**

Genetics

**General rights**

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

**Take down policy**

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact [openaccess@ed.ac.uk](mailto:openaccess@ed.ac.uk) providing details, and we will remove access to the work immediately and investigate your claim.



# Speed of invasion of an expanding population by a horizontally-transmitted trait

Juan Venegas-Ortiz, Rosalind J. Allen, and Martin R. Evans

*SUPA, School of Physics and Astronomy, University of Edinburgh, Mayfield  
Road, Edinburgh EH9 3JZ, United Kingdom*

**Running Title:** Trait spread during range expansion

**Keywords:** wave of advance; Fisher-KPP equation; traveling waves; horizontal transmission; range expansion

**Corresponding author:** M. R. Evans,

SUPA, School of Physics and Astronomy, University of Edinburgh, Mayfield Road, Edinburgh EH9 3JZ, United Kingdom

m.evans@ed.ac.uk

44-131-6505294

## Abstract

Range expansions are a ubiquitous phenomenon, leading to the spatial spread of genetic, ecological, and cultural traits. While some of these traits are advantageous (and hence selected), other, non-selected traits can also spread by hitchhiking on the wave of population expansion as it advances. Understanding current patterns of diversity, and predicting and controlling the effects of future range expansions, requires us to understand how the spread of a hitchhiking trait is coupled to the wave of advance of its host population. Here, we use a coupled Fisher-KPP framework to describe the spread of a horizontally-transmitted hitchhiking trait within a population as it expands. We extend Fisher-KPP wave theory to the coupled system to predict how the hitchhiking trait spreads as a wave within the expanding population. We show that the speed of this trait wave is controlled by an intricate coupling between the tip of the population and trait waves. Our analysis yields a new speed selection mechanism for coupled waves of advance, and reveals the existence of previously unexpected speed transitions. Among other applications, our results may be relevant to understanding patterns of parasite prevalence in colonizing animal populations, and the spread of horizontally-transmitted antibiotic resistance within expanding bacterial populations.

The expansion of a population into a new spatial territory, known as a range expansion, is an important and fundamental process in evolution, ecology and anthropology. Range expansions are driven by selection for advantageous traits, whether these be genetic, ecological, technological or cultural. However, they typically lead to the concomitant spread of other traits, which may not be advantageous but spread by “hitchhiking” with the selected trait. Understanding spatial patterns of genetic, ecological, and cultural diversity requires us to understand how the spread of a hitchhiking trait is coupled to the wave of advance of its host population.

The wave of advance model was introduced by Fisher (Fisher 1937) to describe the spread of an advantageous gene within a spatially extended population, and was used independently by Kolmogorov, Petrovsky and Piskunov (Kolmogorov *et al.* 1937) to describe general growth and diffusion processes, and by Skellam (Skellam 1951) in the ecological context of the invasion of new territory by a colonizing species. This model describes the advance of a population in space with the following equation, which we denote the Fisher-KPP (F-KPP) equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \alpha u(K - u) \quad (1)$$

where  $x$  denotes position and  $t$  time and  $u(x, t)$  is the population density. In this model, population expansion arises from a balance between diffusion of individuals in space (with diffusion constant  $D$ ), and local growth (with maximum population density or carrying capacity  $K$  and linear growth rate  $\alpha K$ ). This equation has extremely broad biological relevance (Ammerman and Cavalli-Sforza 1971, van den Bosch *et al.* 1992, Mollinson 1991, Young and Bettinger 1995, Hethcote 2000, Murray 2004, Ackland *et al.* 2007, Rouzine *et al.* 2008, Barrett-Freeman *et al.* 2008, Greulich *et al.* 2012), and is also important in other fields including applied mathematics (McKean 1975, Merkin and Needham 1989, Merkin and Needham 1993, van Saarlooos 2003), statistical physics (Derrida and Spohn 1988, Brunet and Derrida 1997) and computer science (Majumdar and Krapivsky 2002, Majumdar and Krapivsky 2003). The F-KPP equation predicts that the population advances as a traveling wave with a well-defined speed given by  $v^* = 2\sqrt{\alpha DK}$  for a wide class of initial conditions. This wave speed is determined by a mathematically subtle speed selection principle that depends critically on the population dynamics at the very tip of the wave, as well as the initial condition, and that has been a topic of discussion for more than half a century

(Kolmogorov *et al.* 1937, McKean 1975, Larson 1978, van Saarloos 2003).

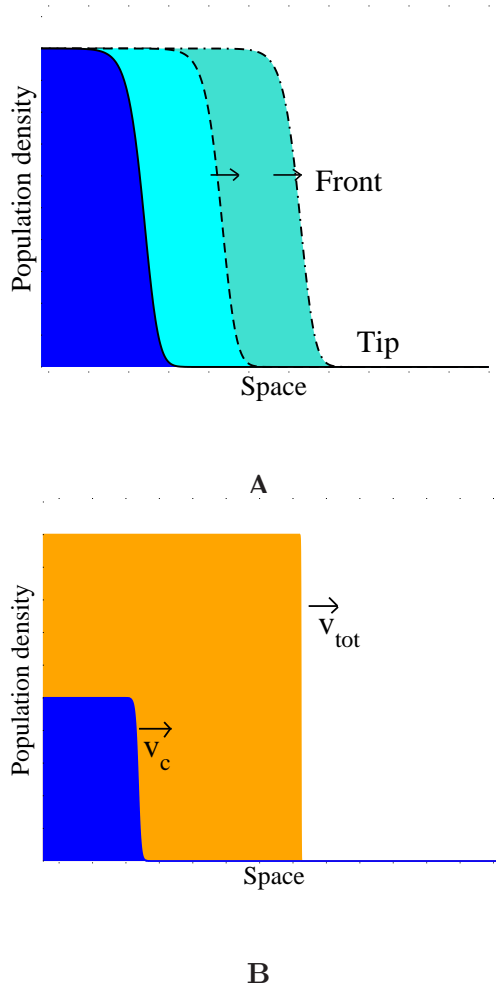


FIG. 1: Propagation of single and coupled F-KPP waves. (a): A population described by the F-KPP equation advances as a traveling wave. The speed of the main part of the wave (the “front”) depends critically on the details of the profile in the tip region, far ahead of the front. (b): The scenario investigated in this study. The sub-populations of individuals with and without the horizontally-transmitted trait are shown in blue and orange, respectively. The total population advances as an F-KPP wave, with speed  $v_{tot} = 2\sqrt{\alpha DK}$ , while the sub-population with the trait also advances as a wave, which lags behind the wave of the total population.

Spatial expansion can have important effects on the genetic structure of a population. In particular, range expansions are often associated with genetic bottlenecks, in which the population of the newly colonized territory is descended from only a few “pioneer” individuals. The resulting spatial patterns of genetic diversity can be used to infer information about past population expansions (Manica *et al.* 2007, Atkinson 2011). Recent work (Klopfstein

*et al.* 2006, Hallatschek *et al.* 2007, Excoffier and Ray 2008, Hallatschek and Nelson 2008, Excoffier *et al.* 2009, Hallatschek and Nelson 2009, Korolev *et al.* 2010) has focused on the amplification of genetic drift at the low-density fronts of expanding populations, strikingly demonstrated in experiments with neutral, fluorescently labelled strains of bacteria and yeast (Hallatschek *et al.* 2007, Hallatschek and Nelson 2009). Range expansion may also favour the maintenance of cooperative traits, both by enrichment of cooperators at the front and by allowing them to outrun non-cooperative cheats (Sen Datta *et al.* 2013).

Population expansions are often accompanied by the spread of non-selected traits which hitchhike with those that are advantageous. These traits may be genetic variants (alleles) which are vertically transmitted and can be gained and lost by mutation or recombination (Maynard Smith and Haigh 1974, Barton 1998, Barton 2000, Etheridge *et al.* 2006). However hitchhiking traits can also be infections, cultural variants or genetic elements that are transmitted horizontally between individuals (Fagan *et al.* 2002, Bar-David *et al.* 2006, Ackland *et al.* 2007). Important examples include parasites carried by an invading population, which may have catastrophic consequences for the native species (Prenter *et al.* 2004, Bar-David *et al.* 2006), or, in some cases be used as a means to control the invaders (Fagan *et al.* 2002); and horizontal gene transfer within spatially structured bacterial communities which presents dangers for the spread of antibiotic resistance, but also opportunities for bioremediation (Molin and Tolker-Nielsen 2003, Fox *et al.* 2008).

The classic case of genetic hitchhiking for vertically-transmitted alleles in well-mixed populations has been the topic of a large body of theory (Maynard Smith and Haigh 1974, Barton 1998, Barton 2000, Etheridge *et al.* 2006). Recently, extensions of this work have shown that spatial structure can have non-trivial effects, typically decreasing the frequency of global selective sweeps that lead to hitchhiking but also possibly favouring hitchhiking by allowing local sweeps (Barton 2000, Barton *et al.* 2013). For horizontally-transmitted traits, the focus of studies so far has mainly been on maintenance of directly selected (or neutral) traits within well-mixed (Lipsitch *et al.* 1995, Bergstrom *et al.* 2000) or spatially structured (Krone *et al.* 2007, Court *et al.* 2013) populations. The situation in which a horizontally-transmitted trait spreads in a population by hitchhiking on selection for a different trait has been addressed in specific ecological and cultural contexts (Fagan *et al.* 2002, Bar-David *et al.* 2006, Ackland *et al.* 2007), but baseline theoretical results remain lacking.

In this paper, we present a baseline model for the spread of a horizontally-transmitted

hitchhiking trait within the wave of advance of an expanding population. Extending Fisher-KPP wave theory to model the coupled waves of advance of the population and the hitchhiking trait, we uncover a new speed selection mechanism which leads to a nontrivial result (our equation (7)) for the speed of advance of the hitchhiking trait. We find that population expansion can significantly affect the speed at which a trait spreads within the population. Our analysis also reveals the existence of abrupt, initial-condition-dependent transitions in the speed of waves of invading traits.

### **Background: Fisher-KPP wave theory**

We begin by reviewing the main results of F-KPP theory for expanding populations. The standard F-KPP equation (1) has traveling wave solutions of the form  $u(x, t) = U(x - vt)$ . At large times the population asymptotically expands in a wave of constant shape which moves at a constant speed  $v$ . A detailed analysis (Kolmogorov *et al.* 1937, McKean 1975, Larson 1978) reveals that the wave speed  $v$  is governed by a simple selection principle which forms the basis of F-KPP wave theory: if the initial profile decays more steeply than  $u(x, 0) \sim e^{-\lambda^*x}$ , where  $\lambda^* = v^*/2D$ , then  $v = v^* = 2\sqrt{\alpha DK}$ ; whereas if  $u(x, 0)$  decays less steeply than  $e^{-\lambda^*x}$  then  $v > v^*$ .

For future reference we review how this result can be understood in a simple way by examining the dynamics of the leading edge of the wave where  $u \ll 1$  (Fig. 1). Then the linearised version of (1)

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \alpha K u \quad (2)$$

exhibits traveling wave solutions with possible velocities  $v \geq v^*$ . The full time-dependent solution of this linearized equation beginning from exponentially decaying initial conditions  $u(x, t = 0) = \exp(-\lambda x)$  for  $x > 0$  can be constructed (van Saarloos 2003). The solution reveals two different, large-time asymptotic regimes (see Supporting Information): the front of the wave (Fig. 1 a) travels with the marginal speed  $v^*$ ; whereas the tip of the wave travels with a higher speed  $v(\lambda) = D\lambda + \alpha K/\lambda$  determined by the initial profile. If  $\lambda > \lambda^* = v^*/(2D)$  the crossover point between the two regimes moves faster than the front and asymptotically the wave travels with speed  $v^*$ . However, if  $\lambda < \lambda^*$  the front catches up with the crossover point and the wave speed is then determined by  $v(\lambda) > v^*$ . Thus for suitably steep initial conditions the marginal speed  $v^*$  is selected. The fact that the



behaviour of the wave at its very tip is crucial in determining its speed has important implications for systems with noise or discrete cutoffs at the tip (Brunet and Derrida 1997, Brunet and Derrida 2001, Hallatschek 2009, Hallatschek 2011).

### Hitchhiking on a wave of advance: coupled F-KPP equations

To model the spread of a horizontally-transmitted hitchhiking trait within an expanding population, we extend the F-KPP framework to consider the dynamics of two sub-populations: sub-population A which carries the trait, and sub-population B which does not. Both sub-populations diffuse in space and replicate, competing for resources. To model horizontal transmission, we suppose that contact between individuals of types A and B can result in both individuals becoming type A. The trait is also lost at a constant rate. Because our aim is to present a baseline model, we assume that there are no fitness differences between the two sub-populations, i.e. that they have equal diffusion constants, growth rates and carrying capacities. Our model is described by the following set of equations:

$$\begin{aligned}\frac{\partial N_A}{\partial t} &= D \frac{\partial^2 N_A}{\partial x^2} + \alpha N_A (K - N_T) - \beta N_A + \gamma N_A N_B \\ \frac{\partial N_B}{\partial t} &= D \frac{\partial^2 N_B}{\partial x^2} + \alpha N_B (K - N_T) + \beta N_A - \gamma N_A N_B ,\end{aligned}\tag{3}$$

where  $N_A(x, t)$  and  $N_B(x, t)$  are the densities of the sub-populations with and without the trait,  $N_T = N_A + N_B$  is the total population density, and  $D$ ,  $K$  and  $\alpha$  are defined as before. The new parameters  $\gamma$  and  $\beta$  control the rates of horizontal transmission and loss of the trait, respectively; these processes exchange individuals between the two subpopulations.

There are three homogeneous density, steady-state solutions of Eqs. (3) which in terms of  $(N_T, N_A)$  read:  $(0, 0)$  (no population);  $(K, 0)$  (population contains no trait carriers) and  $(K, K - \beta/\gamma)$  (coexistence of trait and non-trait subpopulations). The last solution is only physical (i.e. has positive densities) if  $\gamma \geq \beta/K$  i.e. if the rate of horizontal transmission is high enough that the trait can be sustained in the population. In addition to this condition on  $\gamma$  we shall also restrict the parameter values to  $\gamma < \alpha$  so that

$$\alpha > \gamma > \beta/K .\tag{4}$$

The range (4) corresponds to an intermediate transmission rate of the trait, relevant, for example, to the spread of chronic diseases in a colonizing population (Bar-David *et al.* 2006).

Summing the two equations (3) gives a standard F-KPP equation:

$$\frac{\partial N_T}{\partial t} = D \frac{\partial^2 N_T}{\partial x^2} + \alpha N_T (K - N_T), \quad (5)$$

thus the total population advances as a wave, at constant speed  $v_{tot} = 2\sqrt{\alpha DK}$ , determined by the F-KPP speed selection principle (as long as the initial condition decays steeply enough).

To determine the qualitative phenomenology we studied Eqs (3) numerically (see Supporting Information for details). Our simulations (Fig. 1b) reveal that the sub-population of individuals carrying the trait also advances as a traveling wave (which we denote the “trait wave”), but which has a *slower* speed than that of the total population. Thus the trait spreads in space as the population advances, but it lags behind the advancing population. In this paper, we analyze the speed of advance of this “trait wave”, and show that it is controlled by an intricate coupling between the population densities of the two subpopulations at the very tips of the two waves.

An analysis of the linear stability (see Supporting Information) of the three homogeneous fixed point solutions  $(N_T, N_A)$  reveals that under conditions (4),  $(0, 0)$  is unstable,  $(K, 0)$  is a saddle point (one stable and one unstable direction) and  $(K, K - \beta/\gamma)$  is stable. Thus the observed coupled travelling wave solutions correspond to solution  $(0, 0)$  being invaded by solution  $(K, 0)$  (population without trait), and, in turn, solution  $(K, 0)$  being invaded by solution  $(K, K - \beta/\gamma)$  (the coexisting state).

### *Spread of a trait in an established population*

As a point of comparison, we begin with the well-studied case where a horizontally-transmitted, neutral, trait invades an *already established* population. In this case, the total population  $N_T$  is equal to the carrying capacity  $K$  throughout the domain. Setting  $N_T = K$  in Eq. (3) leads to a single F-KPP equation for the spread of the trait:

$$\frac{\partial N_A}{\partial t} = D \frac{\partial^2 N_A}{\partial x^2} + \gamma N_A \left( K - \frac{\beta}{\gamma} - N_A \right). \quad (6)$$

Thus, the trait invades an existing population as a traveling wave with amplitude  $K - \beta/\gamma$  and speed  $v_s = 2\sqrt{D(\gamma K - \beta)}$  predicted by the F-KPP speed selection principle (assuming a sufficiently steep initial condition for sub-population A). Fig. 2 (upper panels) shows numerical simulation results for this scenario.

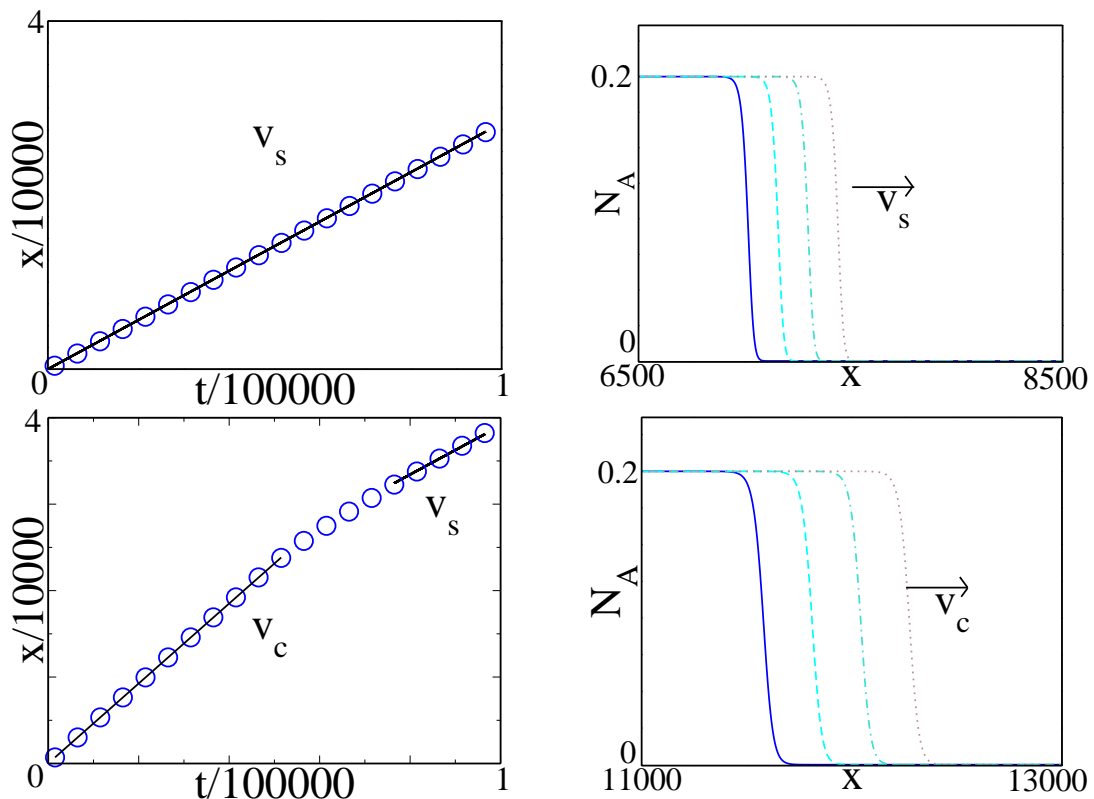


FIG. 2: Invasion of the trait wave into established and expanding populations. The upper panels show numerical simulation results (see Supporting Information) for a trait which invades an already established population, i.e. with initial condition  $N_B = N_T = K$  for  $x > 0$ , while the lower panels show results for invasion of an expanding population, i.e. with initial condition  $N_B = N_T = 0$  for  $x > 0$ . The simulation parameters are identical in the two simulations ( $K = 1, D = 1, \alpha = 1, \beta = 0.08$  and  $\gamma = 0.1$ ). In each case, the right panel shows wave profiles at several different times (the times plotted are the same in the upper and lower panels), while the left panel tracks the position of the wave front as a function of time. The trait wave invades the established population as an F-KPP wave with speed  $v_s$ . It also invades the expanding population as a wave, but with a faster speed  $v_c$ , which eventually transitions to  $v_s$ .

*The trait spreads faster in an expanding population*

We now use our model to investigate what happens when a horizontally-transmitted trait invades a population *as it expands* (Fig. 1b). Fig. 2 (lower panels) shows numerical simulation results, for the same parameter set, but this time starting with the spatial domain initially empty. These simulations clearly show that, after an initial transient (not visible in Fig. 2), the trait advances as a traveling wave whose front moves at a speed  $v_c$

that is *greater* than the speed  $v_s$  at which it invades an already established population – but still less than the speed  $v_{tot}$  of the total population wave. This rapid rate of invasion is maintained for a long time (many times the generation time, given by  $\sim (\alpha K)^{-1}$ ). At very long times, when the total population wave is very far ahead of the trait wave, the speed of the trait wave reverts to  $v_s$  (Fig. 2).

### *Distinctive features of the trait wave*

Based on our understanding of the standard F-KPP wave, we expect the speed of the trait wave to be determined by the dynamics close to the tip. We therefore make a detailed study of this region: Fig. 3(a) shows the profiles of the total population wave and the trait wave, during the time period when the front of the trait wave is moving forward at speed  $v_c$ .

We first zoom in on the region ahead of the total population wave, as indicated by the rightmost circle in Fig. 3(a). Fig. 3(b) shows that the profiles of both the total population and the sub-population with the trait decay exponentially (**note the logarithmic scale on the vertical axis**). In this tip region, we can make an analytical prediction for the speed  $v_{tip}$  at which the tip of the trait wave advances. Because both  $N_A$  and  $N_B$  are very small, with  $N_A \ll N_T$ , we can linearize Eq.(3) to give  $\partial N_A / \partial t = D(\partial^2 N_A / \partial x^2) + N_A(\alpha K - \beta)$ . Then the standard speed selection principle outlined earlier implies that the marginal speed  $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$  is selected and  $N_A(x) \sim \exp[-v_{tip}(x - v_{tip}t)/2D]$ . This prediction is verified by tracking the speed of the very tip of the trait wave in our numerical simulations. Our simulations also show that  $v_{tip} > v_c$  – thus, as for the standard F-KPP wave, the tip of the trait wave advances at a faster speed than its front.

Next, we inspect the trait wave further back in its profile, at the point where it overlaps with the front of the total population wave. This point, shown by the leftmost circle in Fig. 3(a), lies well ahead of the front of trait wave, so that the density of the sub-population with the trait is still very small. Close inspection of our numerical simulations reveals that the trait wave profile has a distinctive “kink” which coincides with the front of the total population wave. This kink, shown in Fig. 3(c), advances with the front of the total population wave: i.e. its speed is  $v_{tot} = 2\sqrt{\alpha DK}$  and its position at time  $t$  is  $x^* = v_{tot}t$ . **As the trait wave front falls behind the total population wave front the trait population density at the kink decreases.**

To summarize, while the trait advances as a traveling wave with speed  $v_c$ , the dynamics

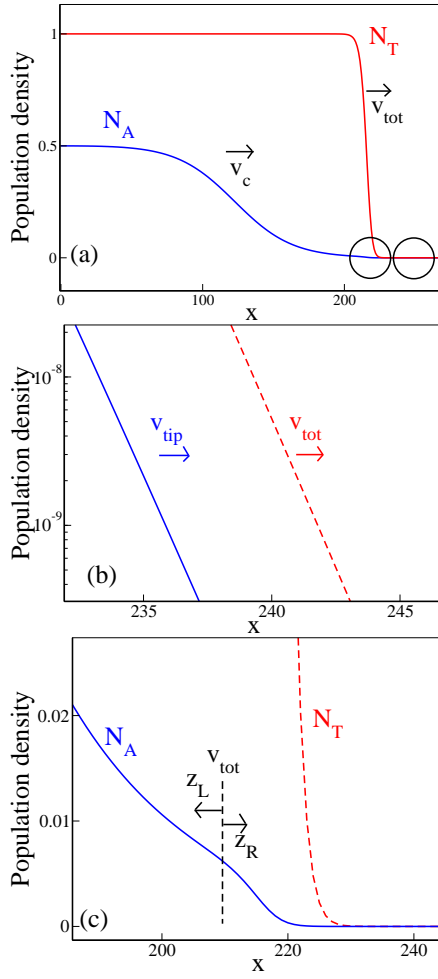


FIG. 3: Detailed features of the profile of the trait wave. Panel (a) shows profiles of the trait wave (blue) and the total population wave (red, dashed), during the time when the trait wave is advancing at speed  $v_c$ . Panel (b) zooms in on the region at the very tip of the two waves (indicated by the right-most circle in panel (a)). Here both profiles decay exponentially (note the log scale on the vertical axis), and the tip of the trait wave advances at speed  $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$ . Panel (c) zooms in on the region of space corresponding to the front of the total population wave (indicated by the left circle in panel (a)), where the trait wave population density is still low. A distinct kink is observed in the trait wave profile  $N_A(x)$ , due to coupling with the total population wave. This kink advances at the speed of the front of the total population wave  $v_{tot} = 2\sqrt{\alpha DK}$ . **The trait population density at the kink decreases in time, as the trait wave front falls behind the total population wave front.** Panel (c) also illustrates the change of coordinate system used to match the asymptotic solutions to the left and right of the kink.

at its tip, where the population density is very small, is rather complex. The tip itself

moves forward at speed  $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$ , but behind the tip the trait wave profile has a kink created by coupling to the front of the total population wave; this kink advances at speed  $v_{tot} = 2\sqrt{\alpha DK}$ . The relative magnitudes of these speeds are  $v_{tot} > v_{tip} > v_c$ .

### Speed selection mechanism for the trait wave

We can obtain an analytic expression for the speed  $v_c$  at which the trait invades an expanding population, by matching asymptotic expansions for the profile of the trait wave on either side of the kink.

Ahead of the kink, we define a coordinate  $z_R = x - v_{tot}t$  which measures the distance from the kink (Fig. 3(c)). Following the result of our earlier analysis of the tip of the trait wave, we expect the profile in this region to decay as  $N_A(z_R, t) \sim \exp[-v_{tip}(z_R + (v_{tot} - v_{tip})t)/(2D)]$ .

Behind the kink, the trait wave advances at speed  $v_c$ . We expect the trait wave profile to increase exponentially with distance behind the kink, so we write  $N_A(z_L, t) \sim \exp[-at + bz_L]$ , where  $z_L = v_{tot}t - x$  measures the distance from the kink and  $a$  and  $b$  are unknown constants such that  $v_c = v_{tot} - a/b$ . By demanding that our two asymptotic expressions must match at the kink: i.e.  $N_A(z_R = 0, t) = N_A(z_L = 0, t)$ , we can determine the constant  $a = v_{tip}(v_{tot} - v_{tip})/(2D)$ . To find the remaining constant  $b$ , we linearize Eq. (3) in the region behind the kink, where the total population is large ( $N_T \approx K$ ), but the amplitude of the trait wave is still small ( $N_A \ll 1$ ). This gives  $\partial N_A / \partial t = D(\partial^2 N_A / \partial x^2) + N_A(\gamma K - \beta)$ . Substituting in our exponential ansatz for  $N_A(z_L, t)$  gives  $b = (1/(2D)) \left( v_{tot} \pm \sqrt{(v_{tot} - v_{tip})^2 + v_{tip}^2 - v_s^2} \right)$ . In order for the inside of the square root to be positive, we need the second condition of (4),  $\alpha > \gamma$ .

This calculation results in two solutions for the speed  $v_c$  of the trait wave, corresponding to the positive and negative square roots in the expression for  $b$ . It turns out that the positive square root gives a speed  $v_c$  which is greater than the speed of the tip  $v_{tip}$ , so we discard that solution. Taking the negative square root, we arrive at the following expression for the speed of the trait wave:

$$v_c = v_{tot} - \frac{v_{tip}(v_{tot} - v_{tip})}{v_{tot} - \sqrt{(v_{tot} - v_{tip})^2 + v_{tip}^2 - v_s^2}} \quad (7)$$

which can be written in terms of the parameters of the model as

$$\frac{v_c}{2\sqrt{D}} = \sqrt{\alpha K} - \frac{\beta - \alpha K + \sqrt{\alpha K(\alpha K - \beta)}}{\sqrt{\alpha K} - \sqrt{(3\alpha - \gamma)K - \beta - 2\sqrt{\alpha K(\alpha K - \beta)}}}. \quad (8)$$

Fig. 4 shows that this prediction is in excellent agreement with our simulation results.

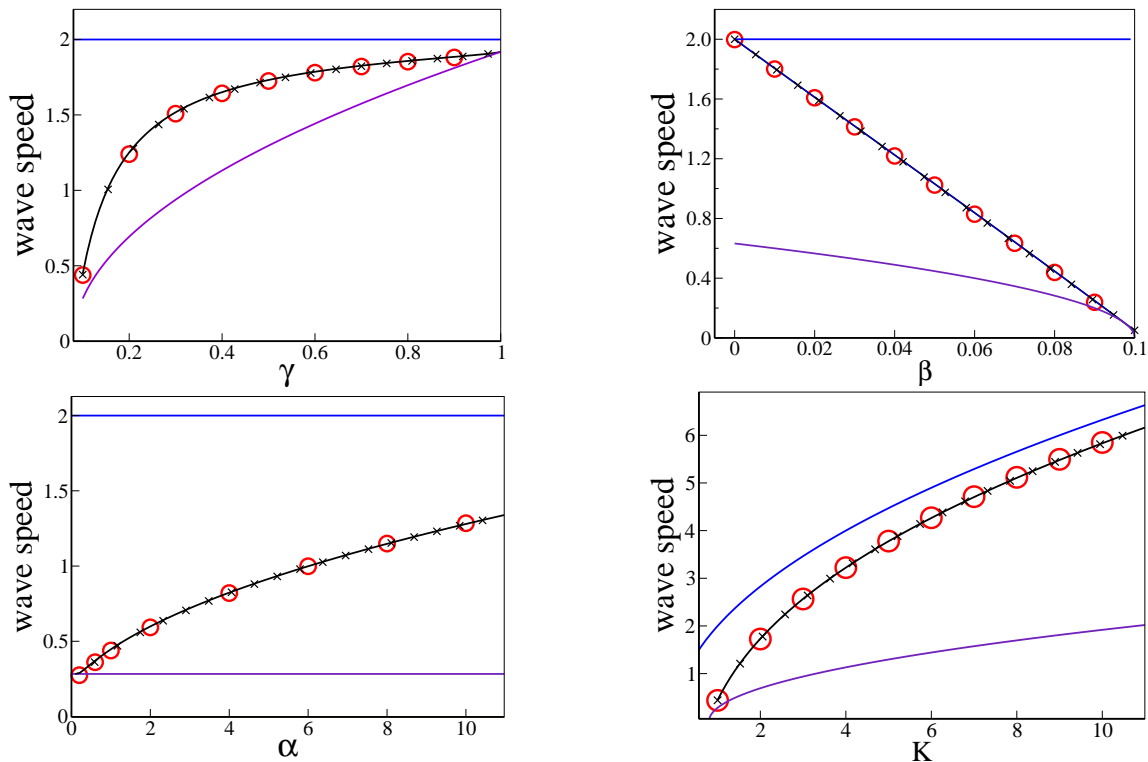


FIG. 4: Analytical prediction, and simulation results, for the speed  $v_c$  of the trait wave as it invades an expanding population. The black lines show the analytical result, Eq (8), while the red circles show simulation results for the trait wave speed and the black crosses show the approximate result, Eq. (9). Except where otherwise indicated on the horizontal axis, the parameters are  $D = \alpha = K = 1.0$ ,  $\gamma = 0.1$ , and  $\beta = 0.08$ . For comparison, the blue lines show the speed of the total population wave  $v_{tot} = 2\sqrt{\alpha DK}$ , while the purple lines show the speed of the trait wave as it invades an established population,  $v_s = 2\sqrt{D(\gamma K - \beta)}$ .

The implications of our result can be understood by noting that in many scenarios we expect that  $\beta \ll \alpha K$ . This can occur either through a low trait loss rate  $\beta$ , or a high growth rate or carrying capacity. Expanding to first order in  $\beta/(\alpha K)$  leads to a simple expression

for the speed of invasion of the trait:

$$\frac{v_c}{v_{tot}} \approx 1 - \frac{\beta}{2\gamma K} \left[ 1 + \sqrt{1 - (\gamma/\alpha)} \right]. \quad (9)$$

Eq. (9) demonstrates that, as we might expect, traits that are poorly transmitted (small  $\gamma$ ) or easily lost (large  $\beta$ ) will lag further behind the main population wave. Importantly, our result also predicts that as the carrying capacity of the population increases, the relative amount by which the trait lags behind the main population wave should decrease. This implies that horizontally-transmitted hitchhiking traits (such as parasites or horizontally transmitted genetic elements) should be found relatively closer to the advancing front in populations with a high carrying capacity, compared to those with a lower carrying capacity.

Our analysis also provides a simple prediction for how much the invasion by the trait is speeded up in an advancing population compared to an established one - i.e. the ratio  $v_c/v_s$ . Expanding for large  $K$  ( $K \gg \beta/\gamma$  and  $\gamma < \alpha$ ) we find that

$$\frac{v_c}{v_s} \approx \left( \frac{\alpha}{\gamma} \right)^{1/2} \left[ 1 - \frac{\beta}{2\gamma K} \left( 1 - \frac{\gamma}{\alpha} \right)^{1/2} \right]. \quad (10)$$

For large carrying capacity  $K$ , relation (10) reduces to  $v_c/v_s \approx (\alpha/\gamma)^{1/2}$ . Thus we expect the spread of a trait in an expanding population to be significantly faster than in an existing population if the birth rate is high and the transmission rate of the trait is low.

## Speed transitions

Interestingly, our simulations also show that horizontally-transmitted hitchhiking traits can undergo abrupt transitions in wave speed (see e.g. Fig. 2, lower panels). These transitions have their origin in the intricate coupling between the trait wave and the total population wave in their tip regions.

### *Slowing down transition due to wave decoupling*

Although the trait wave initially advances at speed  $v_c$ , Fig. 2 shows that eventually it undergoes a slowing-down transition, with a final speed  $v_s$  that equals the speed at which it would invade an established population. Careful inspection of our simulations reveals that this transition occurs when the kink in the trait wave profile (Fig. 3(c)) overtakes its tip - defining the tip as the point at which the density of the trait becomes unresolvable in our numerical simulations. Such a transition is inevitable since the kink advances faster than



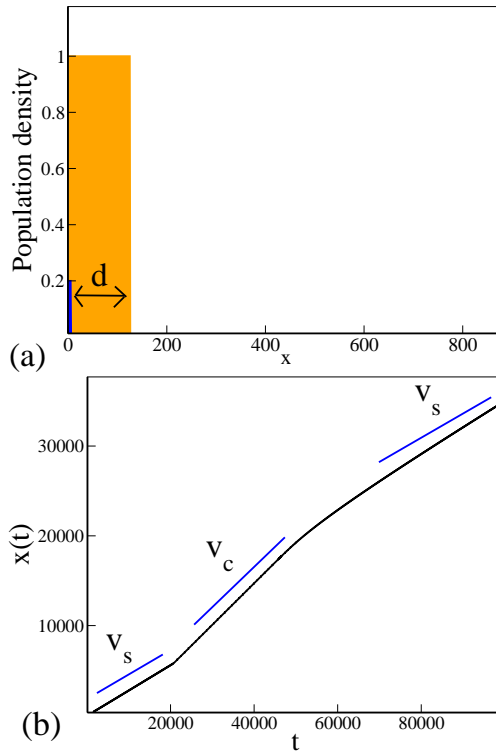


FIG. 5: Initial-condition dependent speeding-up transition. Panel (a) shows the starting point for a simulation in which the spatial domain is initially partially occupied by individuals which do not carry the trait. Here, the initial condition is  $N_B = N_T = K$  for  $0 < x < d$  and  $N_B = N_T = 0$  for  $x > d$ . The subpopulation density  $N_B(x)$  is shown in orange;  $N_A(x)$  is shown in blue. Panel (b) tracks the position of the front of the trait wave as this simulation proceeds. Initially, the trait wave advances at speed  $v_s = 2\sqrt{D(\gamma K - \beta)}$  (as for invasion of an established population). The wave then undergoes an abrupt transition to the faster wave speed  $v_c$  (as given in Eq. (8)). Eventually, the waves become decoupled and the speed reverts to  $v_s$ .

the tip (the tip moves at  $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$  while the kink advances at  $v_{tot} = 2\sqrt{D\alpha K}$ ). When the kink overtakes the tip, the two waves become decoupled at the level of precision of our simulations, and the trait wave behaves as if it were invading an already established population. The time at which this transition happens will of course depend on the details of the initial conditions for the simulations, and on the level of resolution of the tip. However we can predict that this time will scale inversely with the difference in these two speeds, which, for  $\beta/(\alpha K) \ll 1$ , is approximately  $\beta\sqrt{D}/(\alpha K)$ .

*Initial condition-dependent speeding up transition*

Our simulations also reveal that under some circumstances the trait wave can also undergo abrupt *speeding-up* transitions. Fig. 5 shows an example. Here, the spatial domain is partially colonized at the start of the simulation; the region  $0 < x < d$  is occupied by individuals which do not carry the trait, while the rest of the domain is empty (Fig. 5, top panel). During the simulation, the population expands to fill the rest of the domain, while at the same time the trait invades the expanding population.

Fig. 5 (lower panel) tracks the advance of the front of the trait wave in this simulation. Initially, the trait wave front advances at speed  $v_s$ , as if it were invading a fully established population. However, the wave of invasion then makes an abrupt speeding-up transition to the faster speed  $v_c$ . This transition from  $v_s$  to  $v_c$  has its origin in the evolution of the profile of the trait at the start of the simulation. This profile is initially sharp (in our simulations it is a step function). Starting from this steep initial condition, the trait wave develops a tip which, as in standard F-KPP wave theory, advances faster than the wave front (Sherratt 1998a, van Saarloos 2003). Initially this trait wave tip is far behind the front of the total population wave and the trait wave behaves as if it is invading a fully-colonized environment, moving at speed  $v_s$ . However, after some time the tip of the trait wave overtakes the front of the total population wave, and the waves become coupled. At this point, the profile of the trait wave develops a kink, and, following the speed selection mechanism outlined above, its front speed increases to  $v_c$ . Fig. 5 (lower panel) also shows that the wave speed eventually changes back to  $v_s$ , in a slowing-down transition of the type discussed above.

### **Are the observed phenomena biologically relevant?**

The fundamental prediction of our theoretical analysis is that a horizontally-transmitted trait can invade an expanding population significantly faster than it would invade an already established population, but always at a speed slower than the expanding population front. Does this prediction still hold for parameter sets corresponding to real biological scenarios? To test this, we take as a model scenario the invasion of a semi-solid agar matrix by an expanding population of non-motile bacteria which undergo horizontal gene transfer by conjugation. This scenario mimicks the contamination of foodstuff by bacteria (Wimpenny *et al.* 1995, Wilson *et al.* 2002), and also relates to recent experiments on genetic segregation during range expansion (Hallatschek *et al.* 2007, Hallatschek and Nelson 2009). The

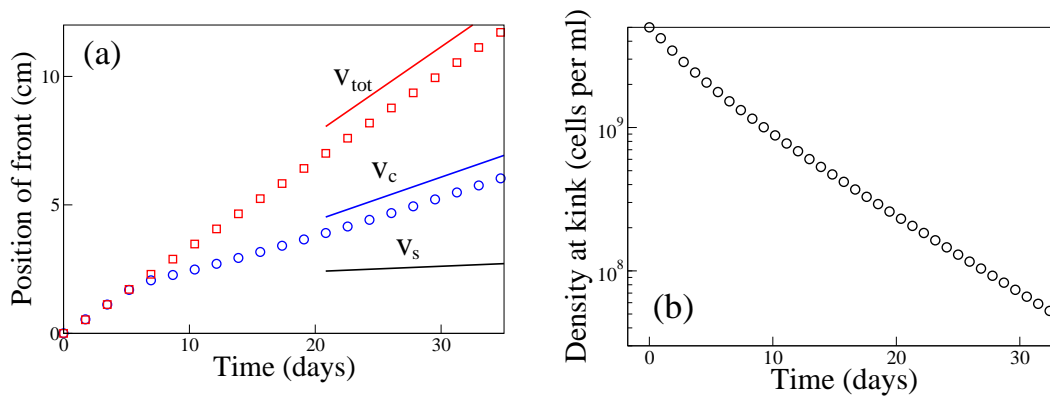


FIG. 6: Numerical simulation results for a parameter set representing the invasion of an agar matrix by a population of non-motile *Escherichia coli* bacteria undergoing horizontal gene transfer by plasmid conjugation. The parameters used were  $D = 1\mu\text{m}^2/\text{s}$ ,  $K = 10^{-2}$  cells/ $\mu\text{m}^3$ ,  $\alpha = 3.85 \times 10^{-2}\mu\text{m}^3/\text{cell}/\text{s}$ ,  $\gamma = 2.8 \times 10^{-4}\mu\text{m}^3/\text{cell}/\text{s}$  and  $\beta = 0.5\gamma K$ . Panel (a): Trajectories of the front positions of the wave of cells without the trait (red squares) and the trait wave (blue circles). Initially, the spatial domain is empty except at its very edge where the two populations take their steady-state values. At early times, the two waves travel together as the travelling wave profiles are established. Thereafter, the trait wave invades the expanding population at the speed  $v_c$  predicted by our theory, which is significantly faster than the speed  $v_s$  with which it would invade an established population ( $v_c$ ,  $v_s$  and  $v_{tot}$  are indicated by the blue, black and red solid lines, respectively). Panel (b): population density of the trait wave at the kink: i.e. at the position of the front of the total population wave (see Figure 3(c)). The trait population density at the kink decreases in time approximately exponentially as the trait wave falls behind the total population wave, but remains significant over the timescale of our simulation (note the log scale on the vertical axis). For reasons of computational speed, these simulations were carried out using standard Euler integration rather than the operator splitting method used in our other calculations (see Supporting Information).

diffusion constant of a non-motile bacterium such as *Escherichia coli* in liquid medium is  $D \approx 1\mu\text{m}^2/\text{s}$  (Berg 1983), and the carrying capacity in rich medium is  $K \approx 10^{10}$  cells/ml (which is equivalent to  $10^{-2}$  cells/ $\mu\text{m}^3$ ). *E. coli* has a doubling time in rich medium of about

30 minutes, so that  $\alpha K = (\ln 2)/30$  per minute (or alternatively  $\alpha = 3.85 \times 10^{-2} \mu\text{m}^3/\text{cell}/\text{s}$ ). The rate of transfer of genetic material (plasmids) by conjugation has been estimated for some strains of *E. coli* as  $\gamma = 10^{-12} \text{ml}/\text{cell}/\text{hour}$  (Simonsen *et al.* 1990) (or equivalently  $\gamma = 2.8 \times 10^{-4} \mu\text{m}^3/\text{cell}/\text{s}$ ). Bacterial plasmid loss rates are highly variable (Summers, 2009). We choose the rate of loss of the horizontally transmitted trait  $\beta = 0.5\gamma K$ , such that in a steady-state, homogeneous population, half the cells are trait carriers.

Fig.6a shows the results of numerical simulations using these parameter values. In these simulations, after an initial transient period, the population advances as two waves, with the wave of trait-carriers (blue circles) lagging behind that of the non-trait carriers (red squares). The speed at which the wave of trait-carrying cells invades the advancing population is indeed well-predicted by our analytical expression for  $v_c$ , Eq. (8), which, for this parameter set, is greater than the speed  $v_s$  at which the trait wave would invade an already established population, by a factor of 8.3. Fig.6b shows the population density of trait-carriers, at the position of the front of the total population wave - i.e. the height of the “kink” in the trait wave (see Fig. 3c). This decreases in time as the trait wave falls behind the total population wave. However, over the time period of our simulation, the population density at the kink remains significant.

In real populations, individuals are of course discrete entities; this leads to a finite lower cutoff for the population density. The fact that, in our continuous simulations, the population density at the kink remains significant for long times (Fig.6b), suggests that our results may be robust to the effects of such a cutoff. To investigate this in more detail, we repeated the simulations of Fig.6, but introducing a cutoff for both the trait-carrying and non-trait carrying subpopulations, at a population density of 1 cell per ml. Fig.7 shows the resulting trajectories for the waves of the two subpopulations. As well as the theoretical speeds  $v_c$ ,  $v_s$  and  $v_{tot}$ , we also indicate the speed  $v_{s,cut}$  at which the trait population invades an already established population, in simulations with the cutoff. Measuring the speed of the trait wave at time 7 days, we find that the trait invades the expanding population 7.2 times faster than it invades the established population. The key prediction of our theory thus still holds in the presence of the cutoff. Fig.7 also shows, however, that the actual magnitude of the trait wave speed is lower than  $v_c$  in the simulations with the cutoff - suggesting that corrections to our theory will be needed to account quantitatively for the effects of population discreteness.

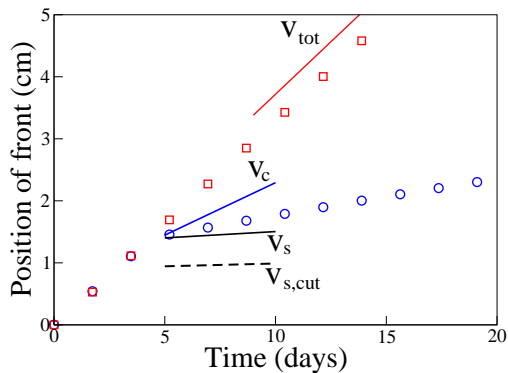


FIG. 7: The effect of a discrete cutoff, for simulations of the invasion of an agar matrix by non-motile *E. coli* bacteria undergoing horizontal gene transfer by plasmid conjugation. The parameters used were as in Figure 6, but with the addition of a cutoff in population density at  $1 \text{ cell/ml} = 10^{-12} \text{ cells}/\mu\text{m}^3$ . In our simulations, subpopulation densities smaller than this value were set to zero. The figure shows the trajectories of the front positions of the wave of cells without the trait (red squares) and the trait wave (blue circles). Initially, the spatial domain is empty except at its very edge where the two populations take their steady-state values. After the initial transient (during which the steady state wave profiles are established), the trait wave invades the expanding population at a speed faster than the predicted speed  $v_s$  for invasion of an established population but slower than the predicted speed  $v_c$ . Also indicated is the speed  $v_{s,cut}$  at which the trait invades an established population in simulations with the same cutoff; this corresponds closely with  $v_s$ . As in Figure 6, these simulations were carried out using standard Euler integration.

## Discussion

The spread of a population in space, and the accompanying spread of genetic, ecological and cultural traits, is a ubiquitous biological phenomenon; correspondingly, the speed selection principle of F-KPP wave theory, which describes the spatial advance of population waves, is one of the most important results in mathematical biology. In this paper, we have presented a baseline model, consisting of coupled F-KPP waves, to describe the spread of a horizontally-transmitted trait within an advancing population. Our results show that in this case, a different speed selection mechanism controls the speed at which the trait in-

vades the expanding population. We have derived an analytic expression (7) for the speed of the trait wave, which reduces to a simple form in the biologically relevant case where the carrying capacity is large. We find that under some circumstances, the trait can invade an expanding population significantly faster than it would spread in a population that is already established. The mechanism underlying this speed-up is that the front of the total population wave creates a kink in the tip region trait wave profile, which couples the two waves at their tips; matching asymptotic solutions on either side of the kink leads to the speed selection mechanism. We also reveal the possibility of abrupt transitions in speed in coupled waves of advance. For a parameter set corresponding to invasion of a semi-solid matrix by a population of *Escherichia coli* bacteria undergoing horizontal gene transfer by conjugation, our theory and simulations suggest that invasion of an expanding population by a horizontally transmitted gene may occur about 8 times faster than invasion of an already established population. While this is a crude model (for example in reality the rate of conjugation may depend on the growth rate (Merkey *et al.* 2011)), it does indicate that our results may indeed be biologically relevant.

An important consideration is the robustness of our results to noise. In real populations, stochastic fluctuations due to births and deaths of individual organisms are inevitable, and can play an important role at the tips of F-KPP waves where population densities are low (Brunet and Derrida 1997, Brunet and Derrida 2001, Hallatschek 2009, Hallatschek 2011). For standard F-KPP waves, finite size effects at the tip of the wave are known to cause a significant correction to the wave speed (Brunet and Derrida 1997). In our model, the kink in the trait wave (which plays a key role in determining its speed) occurs behind the tip, but in the region where the population density of individuals with the trait is still low. In our simulations of Fig.6, the trait population density at the kink remains significant over long times, suggesting that the kink, and the consequent coupling between the waves, would probably survive in the presence of weak noise. This conclusion is also borne out by the fact that we still observe faster invasion of an expanding population than an established one when we include a discrete cutoff (Fig.7). However, the cutoff does significantly affect the speed of the trait wave; likewise in the presence of noise, we would expect the correction of the total population wave speed to carry through into the speed of the trait wave. We hope to study these corrections in more detail in future work.

Coupled systems of reaction-diffusion equations provide a rich source of interesting dy-

namical behavior, from models for infection dynamics, through spatially coupled autocatalytic chemical reaction systems (Merkin and Needham 1993), to advancing fronts of oscillatory predator-prey systems (Sherratt 1998b, Sherratt *et al.* 2009). From a mathematical perspective, for systems of coupled F-KPP waves, the phenomenon of “anomalous spreading”, in which coupling between two populations influences the wave speeds, has been recognized in several examples of systems of coupled F-KPP equations (Weinberger *et al.* 2007, Holzer and Scheel 2012, Holzer 2012). These examples are more complex than the model studied here, in that the diffusion and growth parameters for the two populations are not identical, and the coupling terms are not symmetric. Our study therefore provides a baseline for understanding speed selection in coupled F-KPP waves in general. The asymptotic matching approach presented here should prove useful in understanding these more complex models. Indeed, as a first step towards introducing the effects of selection for or against the horizontally-transmitted trait, we have simulated a version of our model in which we allow the growth rate  $\alpha$  to differ between the two sub-populations. We find that for small growth-rate differences the qualitative results described here remain unchanged (see Supporting Information). Another interesting extension would be to the case where the external environment is spatially heterogeneous; here the range of the “host” population is limited, but may be extended by mutation (Holt and Gomulkiewicz 1997, Kirkpatrick and Barton 1997, Waclaw *et al.* 2010, Greulich *et al.* 2012) or, potentially, by selection for horizontally-transmitted traits.

In conclusion, understanding existing spatial patterns of genetic, ecological or cultural traits, and predicting and controlling the consequences of future population expansions, are important goals for both evolution and ecology. Many of these expansions involve the hitchhiking of horizontally-transmitted traits. The model presented here, while clearly simplistic, reveals important phenomena associated with the spread of traits within expanding population waves, and with coupled systems of F-KPP waves in general, and should provide a basis on which to build more complex and detailed models.

## Acknowledgments

R.J.A. and M.R.E. contributed equally to this paper. The authors thank Davide Marenduzzo for advice on simulation methodology and Jonathan Sherratt for helpful discussions. J.V.-O. was funded by a University of Edinburgh College Studentship. R.J.A. was funded by a

- Ackland, G. J., M. Signitzer, K. Stratford, and M. H. Cohen, 2007 Cultural hitchhiking on the wave of advance of beneficial technologies. *Proc. Natl. Acad. Sci. USA.* 104: 8714-8719.
- Ammerman, A. J., and L. L. Cavalli-Sforza, 1971 Measuring the Rate of Spread of Early Farming in Europe. *Man* 6: 674-688.
- Atkinson, Q. D., 2011 Phonemic diversity supports a serial founder effect model of language expansion from Africa. *Science* 332: 346-349.
  
- Barrett-Freeman, C., M. R. Evans, D. Marenduzzo, and W. C. K. Poon, 2008 Nonequilibrium phase transition in the sedimentation of reproducing particles. *Phys Rev Lett* 101: 100602.
- Barton, N. H., 1998 The effect of hitch-hiking on neutral genealogies. *Gen. Res* 72: 123-133.
- Barton, N. H., 2000 Genetic Hitchhiking. *Phil. Trans. R. Soc. Lond. B* 355: 1553-1562.
- Barton, N. H., A. M. Etheridge, J. Kelleher, and A. Véber, 2013 Genetic hitchhiking in spatially extended populations. *Theor. Pop. Biol.* (in press; available online)
- Bar-David, S., J. O. Lloyd-Smith, and W. M. Getz 2006 Dynamics and management of infectious disease in colonizing populations. *Ecology* 87: 1215-1224.
  
- Berg, H. C., 1983 *Random walks in biology*. Princeton University Press, Princeton, NJ, USA.
- Bergstrom, C. T., M. Lipsitch, and B. R. Levin, 2000 Natural selection, infectious transfer and the existence conditions for bacterial plasmids. *Genetics* 155: 1505-1519.
- van den Bosch, F., R. Hengeveld, and J. A. J. Metz, 1992 Analyzing the velocity of animal range expansion. *Journal of Biogeography* 19: 135-150.
- Brunet E., and B. Derrida, 1997 Shift in the velocity of a front due to a cutoff. *Phys. Rev. E.* 56: 2597-2604.
- Brunet, E., and B. Derrida, 2001 Effect of Microscopic Noise on Front Propagation. *J. Stat. Phys.* 103: 269-282.
- Court, S. J., R. A. Blythe, and R. J. Allen, 2013 Parasites on parasites: Coupled fluctuations in stacked contact processes. *Europhys. Lett.* 101: 50001.



- Derrida B., and H. Spohn, 1988 Polymers on disordered trees, spin glasses and traveling waves. *J. Stat. Phys.* 51: 817-840.
- Etheridge, A., P. Pfaffelhuber, and A. Wakolbinger, 2006 An approximate sampling formula under genetic hitchhiking. *Ann. Appl. Probab.* 16:685-729.
- Excoffier, L., and N. Ray, 2008 Surfing during population expansions promotes genetic revolutions and structuration. *Trends Ecol. Evol.* 23: 347-351.
- Excoffier, L., M. Foll, and R. J. Petit, 2009 Genetic consequences of range expansions. *Rev. Ecol. Evol. Syst.* 40: 481-501.
- Fagan, W. F., M. A. Lewis, M. G. Neubert, and P. van den Driessche, 2002 Invasion theory and biological control. *Ecology Letters* 5: 148-157.
- Fisher, R., 1937 The wave of advance of advantageous gene. *Ann Eugenetic* 7: 353-369.
- Fox, R., X. Zhong, S. M. Krone, and E. M. Top, 2008 Spatial structure and nutrients promote invasion of IncP-1 plasmids in bacterial populations. *ISME J.* 2: 1024-1039.
- Greulich, P., B. Waclaw, and R. J. Allen, 2012 Mutational pathway determines whether drug gradients accelerate evolution of drug-resistant cells. *Phys. Rev. Lett.* 109: 088101.
- Hallatschek, O., P. Hersen, S. Ramanathan, and D. R. Nelson 2007 Genetic drift at expanding frontiers promotes gene segregation. *Proc. Natl. Acad. Sci. USA* 104: 19926-19930.
- Hallatschek, O., and D. R. Nelson, 2008 Gene surfing in expanding populations. *Theor. Popul. Biol.* 73: 158170.
- Hallatschek, O., and D. R. Nelson, 2009 Life at the front of an expanding population. *Evolution* 64: 193206.
- Hallatschek, O., 2011 The noisy edge of traveling waves. *Proc. Natl. Acad. Sci. USA* 108: 1783-1787.
- Hallatschek, O., 2009 Fisher waves in the strong noise limit. *Phys. Rev. Lett.* 103: 108103.
- Hethcote, H. W., 2000 The mathematics of infectious diseases. *SIAM Review* 42: 599-653.
- Holt, R. D., and R. Gomulkiewicz, 1997 The influence of immigration on local adaptation: a re-examination of a familiar paradigm. *Am. Nat.* 149: 563-572
- Holzer M., and A. Scheel, 2012 Accelerated fronts in a two stage invasion process. Preprint.
- Holzer, M., 2012 Anomalous spreading in a system of coupled Fisher-KPP equations. Preprint.
- Kirkpatrick, M., and N. H. Barton, 1997 Evolution of a species' range. *Am. Nat.* 150: 1-23.
- Klopstein, S., M. Currat, and L. Excoffier, 2006 The fate of mutations surfing on the wave of

- a range expansion. *Mol. Biol. Evol.* 23: 482-490.
- Kolmogorov, A., I. Petrovsky, and N. Piskunov, 1937 Study of the diffusion equation with growth of the quantity of matter and its application to a biological problem. *Bull Univ Moscow, Ser Int, Sec A* 1: 1-25.
  - Korolev, K. S., M. Avlund, O. Hallatschek, and D. R. Nelson, 2010 Genetic demixing and evolution in linear stepping stone models. *Rev. Mod. Phys.* 82: 16911718.
  - Krone, S. M., R. Lu, R. Fox, H. Suzuki, and E. M. Top, 2007 Modeling the spatial dynamics of plasmid transfer and persistence. *Microbiology* 153: 2803-2816.
  - Larson, D. A., 1978 Transient bounds and time-asymptotic behaviour of solutions of nonlinear equations of Fisher type. *SIAM J. Appl. Math.* 34: 93-103.
  - Lipsitch, M., M. Nowak, D. Ebert, and R. May, 1995 The population dynamics of vertically and horizontally transmitted parasites. *Proc. R. Soc. London, Ser. B* 260: 321-327
  - Majumdar, S. N., and P. L. Krapivsky, 2002 Extreme value statistics and traveling fronts: Application to computer science. *Phys. Rev. E* 65: 036127.
  - Majumdar, S. N., and P. L. Krapivsky, 2003 Extreme value statistics and traveling fronts: various applications. *Physica A* 318: 161170.
  - Manica, A., W. Amos, F. Balloux, and T. Hanihara, 2007 The effect of ancient population bottlenecks on human phenotypic variation. *Nature* 448: 346-348.
  - Maynard Smith, J., and J. Haigh, 1974 The hitch-hiking effect of a favourable gene. *Genet. Res.* 23: 23-35.
  - McKean, H. P., 1975 Application of Brownian motion to the equation of Kolmogorov-Petrovskii-Piskunov. *Comm. Pure. Appl. Math.* 28: 323-331.
  - Merkey, B. V., L. A. Lardon, J. M. Seoane, J. U. Kreft, and B. F. Smets, 2011 Growth dependence of conjugation explains limited plasmid invasion in biofilms: an individual-based modeling study. *Env. Microbiol.* 13: 2435-2452.
  - Merkin, J. H., and D. J. Needham, 1989 Propagating reaction-diffusion waves in a simple isothermal quadratic autocatalytic chemical system. *J. Eng. Math.* 23: 343-356.
  - Merkin, J. H., D. J. Needham, and S. K. Scott, 1993 Coupled reaction-diffusion waves in an isothermal autocatalytic. chemical system. *IMA J. Appl. Math.* 50: 43-76.
  - Molin, S., and T. Tolker-Nielsen, 2003 Gene transfer occurs with enhanced efficiency in biofilms

- and induces enhanced stabilisation of the biofilm structure. *Curr. Opin. Biotechnol.* 14: 255-261.
- Mollinson, D., 1991 Dependence of epidemic and population velocities on basic parameters. *Mathematical Biosciences* 107: 255-287.
  - Murray, J. D., 2004 *Mathematical Biology, Volume I*. Springer, New York
  - Prenter, J., C. MacNeil, J. T. A. Dick, and A. M. Dunn, 2004 Roles of parasites in animal invasions. *TREE* 19: 385-390.
  - Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery, 1992 *Numerical Recipes in Fortran 77. The Art of Scientific Computing. Second Edition*. Cambridge University Press, Cambridge, pp 827-857.
  - Rouzine, I. M., E. Brunet, and C. O. Wilke, 2008 The traveling-wave approach to asexual evolution: Muller's ratchet and speed of adaptation. *Theoretical population biology* 73: 24-46.
  - van Saarloos, W., 2003 Front propagation into unstable states. *Phys. Rep.* 386: 29-222.
  - Sen Datta, M., K. S. Korolev, I. Cvijovic, C. Dudley, and J. Gore, 2013 Range expansion promotes cooperation in an experimental microbial metapopulation *Proc. Natl. Acad. Sci. USA* (early edition)
  - Sherratt, J. A., 1998a On the transition from initial data to travelling waves in the F-KPP equation. *Dyn. Stab. Syst.* 13: 167-174.
  - Sherratt, J. A., 1998b Invading wave fronts and their oscillatory wakes are linked by a modulated travelling phase resetting wave. *Physica D* 117: 145-166.
  - Sherratt, J. A., M. J. Smith, and D. M. Radenacher, 2009 Locating the transition from Periodic oscillations to spatiotemporal chaos in the wake of invasion. *Proc. Natl. Acad. Sci. USA* 106: 10890-10895.
  - Simonsen, L., D. M. Gordon, F. M. Stewart, and B. R. Levin, 1990 Estimating the rate of plasmid transfer: an end-point method. *J. Gen. Microbiol.* 136: 2319-2325.
  - Skellam, J. G. 1951 Random dispersals in theoretical populations. *Biometrika* 38: 196-218.
  - Summers, D. K., 2009 *The biology of plasmids*. Blackwell Publishing Ltd, Oxford, UK.
  - Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie, and A. M. Kuris, 2003 Introduced species and their missing parasites. *Nature* 421: 628-630.
  - Waclaw, B., R. J. Allen, and M. R. Evans, 2010 A dynamical phase transition in a model for

evolution with migration. *Phys. Rev. Lett.* 105: 268101.

- Weinberger, H. F., M. A. Lewis, and B. Li, 2007 Anomalous spreading speeds of cooperative recursion systems. *J. Math. Biol.* 55: 207-222.
  
- Wilson, P. D. G., T. F. Brocklehurst, S. Arino, D. Thuault, M. Jakobsen, M. Lange, J. Farkas, J. W. T. Wimpenny, and J. F. van Impe, 2002 Modelling microbial growth in structured foods: towards a unified approach. *Int. J. Food Microbiol.* 73: 275-289.
  
- Wimpenny, J. W. T., L. Leistner, L. V. Thomas, A. J. Mitchell, K. Katsaras, and P. Peetz, 1995 Submerged bacterial colonies within food and model systems: their growth, distribution and interactions. *Int. J. Food Microbiol.* 28: 299-315.
  
- Young, D. A., and R. L. Bettinger, 1995 Simulating the global human expansion in the Late Pleistocene. *J. Archeological Sci.* 22: 89-92.