Speed Selection in Coupled Fisher Waves

Martin R. Evans

SUPA, School of Physics and Astronomy, University of Edinburgh, U.K.

September 13, 2013

Collaborators:
Juan Venegas-Ortiz, Rosalind Allen

Plan: Speed Selection in Coupled Fisher Waves

Plan

I Recap of Fisher equation, travelling waves + speed selection principle

II Coupled Fisher waves + new speed selection mechanism

References:

J. Venegas-Ortiz, R. J. Allen and M.R. Evans (2013)

I Fisher-KPP Equation (1d)

Population density $u(x,t)$ obeys

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

- Fisher (1937) - *The wave of advance of advantageous gene*
- Kolmogorov, Petrovsky, Piskunov (1937) *Study of the diffusion equation with growth of the quantity of matter and its application to a biological problem.*
- Skellam (1951) *Random dispersals in theoretical populations.*

Basically a nonlinear diffusion equation - nonlinearity is growth with saturation

Linear growth rate αK, Carrying capacity K

I Fisher-KPP Equation (1d)

Population density $u(x,t)$ obeys

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

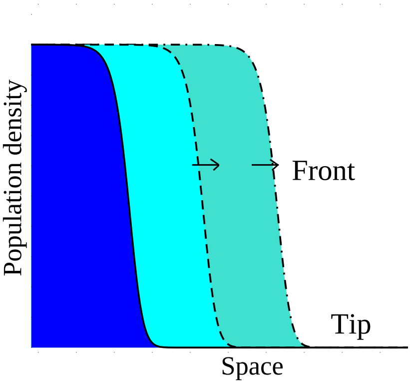
- Fisher (1937) - *The wave of advance of advantageous gene*
- Kolmogorov, Petrovsky, Piskunov (1937) *Study of the diffusion equation with growth of the quantity of matter and its application to a biological problem.*
- Skellam (1951) *Random dispersals in theoretical populations.*

Basically a nonlinear diffusion equation - nonlinearity is growth with saturation

Linear growth rate αK, Carrying capacity K

Appears ubiquitously in: disordered systems such as Directed Polymers in random media; nonequilibrium systems such as directed percolation; computer science search problems etc

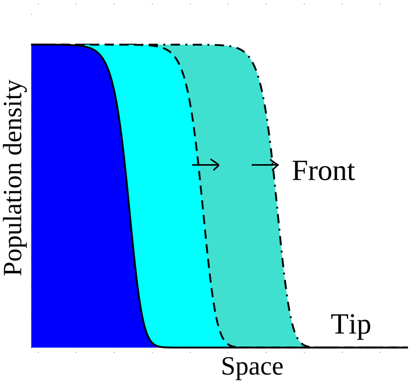
Travelling Wave Solutions



Nonlinear wave with finite width travelling at speed v.

Stable f.p. solution $u = K$ invades unstable f.p. solution $u = 0$

Travelling Wave Solutions



Nonlinear wave with finite width travelling at speed v.

Stable f.p. solution $u = K$ invades unstable f.p. solution $u = 0$

Speed selection principle

The selected speed of the front is determined by tip dynamics and initial conditions

Physical Examples

Ordering Dynamics e.g. Time-dependent Landau-Ginzburg equation

$$\frac{\partial m}{\partial t} = D\nabla^2 m - \frac{\partial}{\partial m} f(m) \qquad f(m) = -am^2 + bm^4$$

Contact Process

$$\begin{array}{rcll} 1 & \rightarrow & 0 & \text{rate} \quad 1 \\ 01 & \rightarrow & 11 & \text{rate} \quad \lambda \\ 10 & \rightarrow & 11 & \text{rate} \quad \lambda \end{array}$$

Mean field for density ρ_i

$$\begin{aligned} \frac{\partial \rho_i}{\partial t} &= -\rho_i + \lambda(1-\rho_i)\rho_{i+1} + \lambda\rho_{i-1}(1-\rho_i) \\ \rightarrow \frac{\partial \rho}{\partial t} &\simeq \lambda \frac{\partial^2 \rho}{\partial x^2} + (2\lambda - 1)\rho - 2\lambda\rho^2 \end{aligned}$$

Generally stable phase (fixed point) invades unstable phase (fixed point)

Speed Selection Principle (physics approach) I

Simple Linear Analysis: linearise at tip $u \ll 1$

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

Speed Selection Principle (physics approach) I

Simple Linear Analysis: linearise at tip $u \ll 1$

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

Try wave solution $u(x,t) = f(z)$ where $z = x - vt$

$$-vf' = Df'' + \alpha K f$$

Exponential solutions $f = \mathrm{e}^{-\lambda z}$ where $v\lambda = D\lambda^2 + \alpha K$.
Solve for λ

$$\lambda = \frac{v \pm (v^2 - 4\alpha D K)^{1/2}}{2D}$$

Real if

$$v > v^* = 2\sqrt{\alpha D K}$$

Speed Selection Principle (physics approach) I

Simple Linear Analysis: linearise at tip $u \ll 1$

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

Try wave solution $u(x,t) = f(z)$ where $z = x - vt$

$$-vf' = Df'' + \alpha K f$$

Exponential solutions $f = \mathrm{e}^{-\lambda z}$ where $v\lambda = D\lambda^2 + \alpha K$.
Solve for λ

$$\lambda = \frac{v \pm (v^2 - 4\alpha D K)^{1/2}}{2D}$$

Real if

$$v > v^* = 2\sqrt{\alpha D K}$$

Speed selection principle

The marginal speed v^* is selected for sufficiently steep initial conditions.

Speed Selection Principle II:

More involved Linear Analysis

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

Solve for initial condition $u(x,0) = \mathrm{e}^{-\lambda x}$ for $x \geq 0$:

$$u(x,t) = (1/2)e^{-\lambda(x - v(\lambda)t)}\left[1 + \mathrm{erf}\Big((x - 2D\lambda t)/(2\sqrt{Dt})\Big)\right]$$

where

$$v(\lambda) = D\lambda + \frac{\alpha K}{\lambda}\ .$$

Speed Selection Principle II:

More involved Linear Analysis

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

Solve for initial condition $u(x,0) = \mathrm{e}^{-\lambda x}$ for $x \geq 0$:

$$u(x,t) = (1/2)e^{-\lambda(x-v(\lambda)t)}\left[1 + \mathrm{erf}\Big((x - 2D\lambda t)/(2\sqrt{Dt})\Big)\right]$$

where

$$v(\lambda) = D\lambda + \frac{\alpha K}{\lambda}\ .$$

Far tip $x \gg 2D\lambda t$

Use $\mathrm{erf}(z) \simeq 1$ for $z \gg 1 \Rightarrow \quad u(x,t) \simeq \exp\left[-\lambda(x - v(\lambda)t\right]$

Thus the tip speed is $v(\lambda)$

Speed Selection Principle II:

More involved Linear Analysis

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

Solve for initial condition $u(x,0) = \mathrm{e}^{-\lambda x}$ for $x \geq 0$:

$$u(x,t) = (1/2)e^{-\lambda(x-v(\lambda)t)}\left[1 + \mathrm{erf}\Big((x - 2D\lambda t)/(2\sqrt{Dt})\Big)\right]$$

where

$$v(\lambda) = D\lambda + \frac{\alpha K}{\lambda}\ .$$

Far tip $x \gg 2D\lambda t$

Use $\mathrm{erf}(z) \simeq 1$ for $z \gg 1 \Rightarrow \quad u(x,t) \simeq \exp\left[-\lambda(x - v(\lambda)t\right]$

Thus the tip speed is $v(\lambda)$

Front $x \ll 2D\lambda t$

Use $\mathrm{erf}(-z) \simeq -1 + \dfrac{\mathrm{e}^{-z^2}}{z\sqrt{\pi}}$ for $z \gg 1$

$\Rightarrow \quad u \simeq \exp\left[-\lambda^*(x - v^* t) - (x - v^* t)^2/(4Dt)\right]$

where $v^* = 2(D\alpha K)^{1/2}$.

Speed Selection Principle III:

Crossover point between far tip and front regimes $x = 2D\lambda t$.

If $\lambda > \lambda^* = v^*/2D$ (steep i.c.), then the crossover point advances faster than the tip, and "front" has speed v^*.

If $\lambda < \lambda^*$, the front catches up with crossover point which falls behind tip, the speed of the front will be controlled by the tip $v(\lambda)$.

Speed Selection Principle III:

Crossover point between far tip and front regimes $x = 2D\lambda t$.

If $\lambda > \lambda^* = v^*/2D$ (steep i.c.), then the crossover point advances faster than the tip, and "front" has speed v^*.

If $\lambda < \lambda^*$, the front catches up with crossover point which falls behind tip, the speed of the front will be controlled by the tip $v(\lambda)$.

Speed selection principle

- If the initial profile decays faster than $u(x,0) \sim \mathrm{e}^{-\lambda^* x}$, where $\lambda^* = v^*/2D$, then wave travels at marginal speed $v = v^* = 2\sqrt{\alpha D K}$
- If the initial profile decays less steeply, say as $\mathrm{e}^{-\lambda x}$ where $\lambda < \lambda^*$, the wave advances at faster speed $v(\lambda) = D\lambda + \alpha K/\lambda$.

Propagation of coupled Fisher-KPP waves

Motivation

- Horizontal gene transfer within bacterial population
- More generally acquisation of trait $\Rightarrow$ two sub populations N_A and N_B: those with trait and those with without

Propagation of coupled Fisher-KPP waves

Motivation

- Horizontal gene transfer within bacterial population
- More generally acquisation of trait $\Rightarrow$ two sub populations N_A and N_B: those with trait and those with without

$$
\begin{aligned}
(1) \quad \frac{\partial N_{\rm A}}{\partial t} &= D\frac{\partial^2 N_{\rm A}}{\partial x^2} + \alpha N_{\rm A}(K - N_{\rm T}) - \beta N_{\rm A} + \gamma N_{\rm A} N_{\rm B} \; , \\
(2) \quad \frac{\partial N_{\rm B}}{\partial t} &= D\frac{\partial^2 N_{\rm B}}{\partial x^2} + \alpha N_{\rm B}(K - N_{\rm T}) + \beta N_{\rm A} - \gamma N_{\rm A} N_{\rm B}
\end{aligned}
$$

$N_{\rm T} = N_{\rm A} + N_{\rm B}$ is the total population density

New parameters

γ rate of horizontal transmission of trait

β loss rate of trait

Propagation of coupled Fisher-KPP waves

Motivation

- Horizontal gene transfer within bacterial population
- More generally acquisation of trait $\Rightarrow$ two sub populations N_A and N_B: those with trait and those with without

$$(1) \quad \frac{\partial N_{\mathrm{A}}}{\partial t} = D\frac{\partial^2 N_{\mathrm{A}}}{\partial x^2} + \alpha N_{\mathrm{A}}(K - N_{\mathrm{T}}) - \beta N_{\mathrm{A}} + \gamma N_{\mathrm{A}} N_{\mathrm{B}} \ ,$$

$$(2) \quad \frac{\partial N_{\mathrm{B}}}{\partial t} = D\frac{\partial^2 N_{\mathrm{B}}}{\partial x^2} + \alpha N_{\mathrm{B}}(K - N_{\mathrm{T}}) + \beta N_{\mathrm{A}} - \gamma N_{\mathrm{A}} N_{\mathrm{B}}$$

$N_{\mathrm{T}} = N_{\mathrm{A}} + N_{\mathrm{B}}$ is the total population density

New parameters

γ rate of horizontal transmission of trait $\qquad$ β loss rate of trait

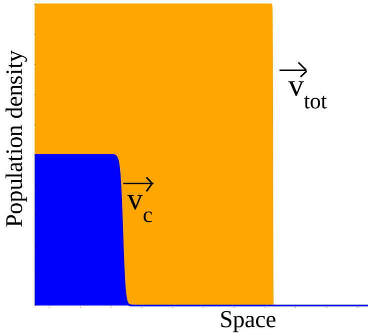
Summing (1,2) gives a standard Fisher-KPP equation:

$$(3) \quad \frac{\partial N_{\mathrm{T}}}{\partial t} = D\frac{\partial^2 N_{\mathrm{T}}}{\partial x^2} + \alpha N_{\mathrm{T}}(K - N_{\mathrm{T}}) \ , \qquad \text{with speed} \quad v_{\mathrm{T}} = 2\sqrt{\alpha K D}$$

Propagation of coupled Fisher-KPP waves

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

Numerics reveal



i.e. an invading population wave which does not carry the trait in turn being invaded by a 'trait wave' with different speed

Fixed point Structure

$$\begin{aligned}\frac{\partial N_{\mathrm{A}}}{\partial t} &= D\frac{\partial^2 N_{\mathrm{A}}}{\partial x^2} + \alpha N_{\mathrm{A}}(K - N_{\mathrm{T}}) - \beta N_{\mathrm{A}} + \gamma N_{\mathrm{A}} N_{\mathrm{B}}\ , \\ \frac{\partial N_T}{\partial t} &= D\frac{\partial^2 N_T}{\partial x^2} + \alpha N_{\mathrm{T}}(K - N_{\mathrm{T}})\end{aligned}$$

Choose intermediate transmission rate $\alpha > \gamma > \beta/K$.

There are three homogeneous density, steady-state solutions (N_T^*, N_A^*) with dynamical stabilities:

- The fixed point $(N_T^*, N_A^*) = (0, 0)$ is unstable.
- $(N_T^*, N_A^*) = (K, 0)$ is a saddle point.
- $(N_T^*, N_A^*) = (K, K - \beta/\gamma)$ is stable

Fixed point Structure

$$
\begin{aligned}
\frac{\partial N_{\mathrm{A}}}{\partial t} &= D\frac{\partial^2 N_{\mathrm{A}}}{\partial x^2} + \alpha N_{\mathrm{A}}(K - N_{\mathrm{T}}) - \beta N_{\mathrm{A}} + \gamma N_{\mathrm{A}} N_{\mathrm{B}}\ , \\
\frac{\partial N_T}{\partial t} &= D\frac{\partial^2 N_T}{\partial x^2} + \alpha N_{\mathrm{T}}(K - N_{\mathrm{T}})
\end{aligned}
$$

Choose intermediate transmission rate $\alpha > \gamma > \beta/K$.

There are three homogeneous density, steady-state solutions (N_T^*, N_A^*) with dynamical stabilities:

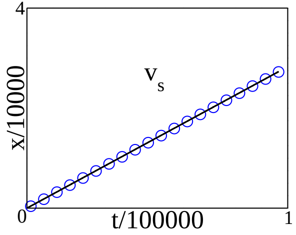
- The fixed point $(N_T^*, N_A^*) = (0, 0)$ is unstable.
- $(N_T^*, N_A^*) = (K, 0)$ is a saddle point.
- $(N_T^*, N_A^*) = (K, K - \beta/\gamma)$ is stable

The coupled travelling waves we observe correspond to a homogeneous spatial domain of $(0, 0)$ being invaded by the solution $(K, 0)$ being invaded by the solution $(K, K - \beta/\gamma)$ (i.e. the trait wave).

Effect of different initial conditions

Spread of trait in established Population

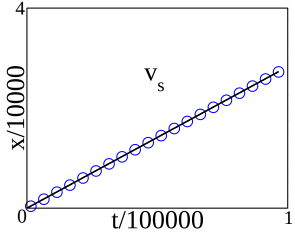
Initially $N_T = K$ throughout the domain (and remains so)



Effect of different initial conditions

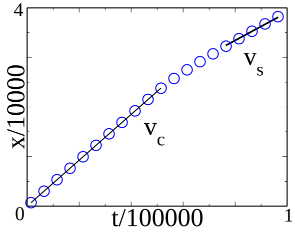
Spread of trait in established Population

Initially $N_{\mathrm{T}} = K$ throughout the domain (and remains so)



Spread of trait in expanding population

Domain initially empty $N_T = 0$.



Summary of different speeds I

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- v_s speed of trait wave invading saturated population ($N_T = K$)
- v_c speed of trait wave invading expandng population

Summary of different speeds I

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- v_s speed of trait wave invading saturated population ($N_T = K$)
- v_c speed of trait wave invading expandng population

  also we have
- $v_{\rm tip}$ speed of far tip of trait wave (N_A, $N_T \ll 1$)

Summary of different speeds I

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- v_s speed of trait wave invading saturated population ($N_T = K$)
- v_c speed of trait wave invading expandng population

  also we have
- $v_{\rm tip}$ speed of far tip of trait wave (N_A, $N_T \ll 1$)

v_s : Set $N_T = K$ yields F-KPP equation

$$\frac{\partial N_{\rm A}}{\partial t} = D\frac{\partial^2 N_{\rm A}}{\partial x^2} + \gamma N_{\rm A}\left(K - \frac{\beta}{\gamma} - N_{\rm A}\right) .$$

Thus usual speed selection predicts $v_s = 2\sqrt{D(\gamma K - \beta)}$

Summary of different speeds I

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- v_s speed of trait wave invading saturated population ($N_T = K$)
- v_c speed of trait wave invading expandng population

  also we have
- $v_{\rm tip}$ speed of far tip of trait wave (N_A, $N_T \ll 1$)

v_s : Set $N_T = K$ yields F-KPP equation

$$\frac{\partial N_{\rm A}}{\partial t} = D\frac{\partial^2 N_{\rm A}}{\partial x^2} + \gamma N_{\rm A}\left(K - \frac{\beta}{\gamma} - N_{\rm A}\right) \ .$$

Thus usual speed selection predicts $v_s = 2\sqrt{D(\gamma K - \beta)}$

v_{tip} : Set N_T, $N_A \ll 1$ and linearise

$$\frac{\partial N_{\rm A}}{\partial t} = D\frac{\partial^2 N_{\rm A}}{\partial x^2} + N_{\rm A}\left(\alpha K - \beta\right) \ .$$

Thus usual speed selection predicts $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$

Summary of different speeds II

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- $v_s = 2\sqrt{D(\gamma K - \beta)}$ speed of trait wave invading saturated population ($N_T = K$)
- $v_{\rm tip} = 2\sqrt{D(\alpha K - \beta)}$ speed of far tip of trait wave (N_A, $N_T \ll 1$)

Summary of different speeds II

- $v_T = 2\sqrt{D\alpha K}$ speed of total population wave
- $v_s = 2\sqrt{D(\gamma K - \beta)}$ speed of trait wave invading saturated population ($N_T = K$)
- $v_{\rm tip} = 2\sqrt{D(\alpha K - \beta)}$ speed of far tip of trait wave (N_A, $N_T \ll 1$)

We show that

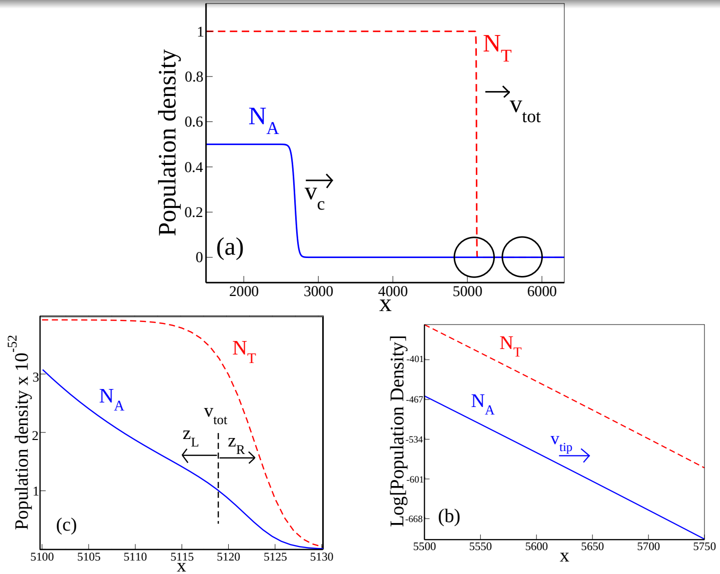
Speed of trait wave invading expandng population

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

- **N.B.**

$$v_T > v_{\rm tip} > v_c > v_s$$

Determination of v_c: the kink in the trait wave



Kink at $x = v_T t$

Far tip at $x >> v_T t$

Speed selection mechanism for the trait wave

Ahead of kink

Linearise N_{A}, $N_{\mathrm{B}} \ll 1$ to get $\partial N_{\mathrm{A}}/\partial t = D(\partial^2 N_{\mathrm{A}}/\partial x^2) + N_{\mathrm{A}}(\alpha K - \beta)$

Then $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$ is selected and defining $z_{\mathrm{R}} = x - v_T t$ we get

$$N_{\mathrm{A}}(z_{\mathrm{R}}, t) \sim \exp[-v_{\mathrm{tip}}(z_{\mathrm{R}} + (v_T - v_{\mathrm{tip}})t)/(2D)$$

Speed selection mechanism for the trait wave

Ahead of kink

Linearise N_{A}, $N_{\mathrm{B}} \ll 1$ to get $\partial N_{\mathrm{A}}/\partial t = D(\partial^2 N_{\mathrm{A}}/\partial x^2) + N_{\mathrm{A}}(\alpha K - \beta)$

Then $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$ is selected and defining $z_{\mathrm{R}} = x - v_T t$ we get

$$N_{\mathrm{A}}(z_{\mathrm{R}}, t) \sim \exp[-v_{\mathrm{tip}}(z_{\mathrm{R}} + (v_T - v_{\mathrm{tip}})t)/(2D)$$

Behind kink

Write

$$N_{\mathrm{A}}(z_{\mathrm{L}}, t) \sim \exp[-at + bz_{\mathrm{L}}]$$

,
where $z_{\mathrm{L}} = v_T t - x$ and a and b are unknown constants such that

$$v_c = v_T - a/b$$

Speed selection mechanism for the trait wave

Ahead of kink

Linearise N_{A}, $N_{\mathrm{B}} \ll 1$ to get $\partial N_{\mathrm{A}}/\partial t = D(\partial^2 N_{\mathrm{A}}/\partial x^2) + N_{\mathrm{A}}(\alpha K - \beta)$

Then $v_{tip} = 2\sqrt{D(\alpha K - \beta)}$ is selected and defining $z_{\mathrm{R}} = x - v_T t$ we get

$$N_{\mathrm{A}}(z_{\mathrm{R}}, t) \sim \exp[-v_{\mathrm{tip}}(z_{\mathrm{R}} + (v_T - v_{\mathrm{tip}})t)/(2D)$$

Behind kink

Write

$$N_{\mathrm{A}}(z_{\mathrm{L}}, t) \sim \exp[-at + bz_{\mathrm{L}}]$$

,
where $z_{\mathrm{L}} = v_T t - x$ and a and b are unknown constants such that

$$v_c = v_T - a/b$$

By demanding that our two asymptotic expressions must match at the kink: i.e. $N_{\mathrm{A}}(z_{\mathrm{R}} = 0, t) = N_{\mathrm{A}}(z_{\mathrm{L}} = 0, t)$, we can determine

$$a = v_{\mathrm{tip}}(v_T - v_{\mathrm{tip}})/(2D)$$

Speed selection mechanism for the trait wave II

To find the remaining constant b, we linearize in the region behind the kink, where the total population is large ($N_{\mathrm{T}} \approx K$), but the amplitude of the trait wave is still small ($N_{\mathrm{A}} \ll 1$). This gives

$$\partial N_{\mathrm{A}}/\partial t = D(\partial^2 N_{\mathrm{A}}/\partial x^2) + N_{\mathrm{A}}(\gamma K - \beta)$$

But now we need a new selection mechanism for solution

Substituting in $N_{\mathrm{A}}(z_{\mathrm{L}}, t) \sim \exp[-at + bz_{\mathrm{L}}]$ with a now determined by matching gives a quadratic for b with root

$$b = (1/(2D)) \left(v_T - \sqrt{(v_T - v_{tip})^2 + v_{tip}^2 - v_s^2} \right)$$

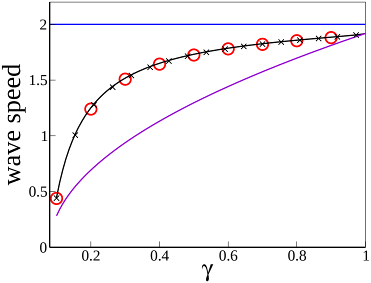
.
Using

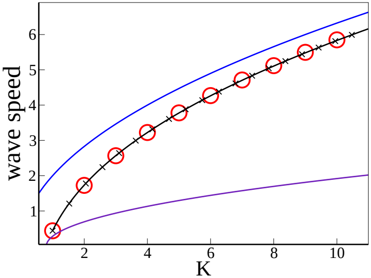
$$v_c = v_T - a/b$$

we finally obtain the following expression for the speed of the trait wave:

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

Analytical prediction and simulation results for the speed v_c of the trait wave





The black lines show the analytical result while the red circles show simulation results for the trait wave speed

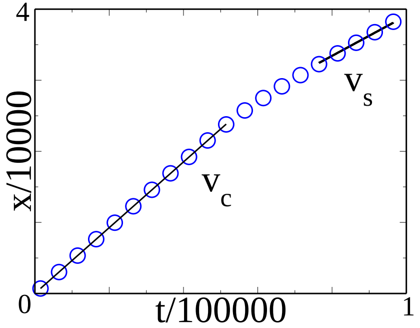
For comparison the blue lines show the speed of the total population wave $v_T = 2\sqrt{\alpha D K}$ while the purple lines show the speed of the trait wave as it invades an established population, $v_s = 2\sqrt{D(\gamma K - \beta)}$.

Recap: Spread of trait in expanding population

Consider an *expanding population* starting with the spatial domain initially empty.

Recap: Spread of trait in expanding population

Consider an *expanding population* starting with the spatial domain initially empty.

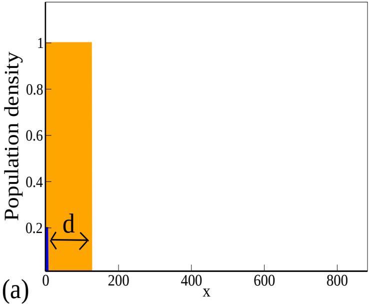


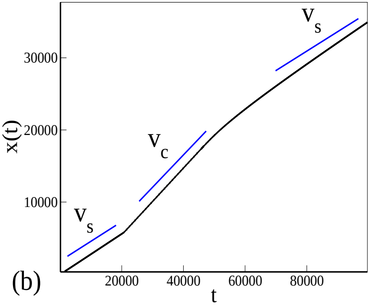
Invasion of Expanding Population

Clearly the trait wave advances at speed v_c that is *greater* than the speed v_s at which it invades an established population – but still less than the speed v_T of the total population wave.

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

Initial-condition dependent speeding-up transition





Initially system partially occupied by non-trait population.

Summary

Summary

- Fisher-KPP equation exhibits nonlinear travelling waves
- We study coupled Fisher waves and find new selection mechanism

Summary

Summary

- Fisher-KPP equation exhibits nonlinear travelling waves
- We study coupled Fisher waves and find new selection mechanism

Outlook

- Many other generalisations to coupled Fisher waves remain to be studied
- Important to consider effect of noise