Invasion speeds in a competition-diffusion model with mutation

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Joint work with

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Competition-diffusion-mutation model

- consider model of two phenotypes of a species

$$\frac{\partial n_e}{\partial t} = D_e \frac{\partial^2 n_e}{\partial x^2} + r_e n_e(1 - m_{ee} n_e - m_{ed} n_d) - \mu e\, n_e + \mu d\, n_d$$
$$\frac{\partial n_d}{\partial t} = D_d \frac{\partial^2 n_d}{\partial x^2} + r_d n_d(1 - m_{de} n_e - m_{dd} n_d) + \mu e\, n_e - \mu d\, n_d$$

where

- n_e, n_d = densities of two phenotypes of a single species
- D_e, D_d = dispersal rates
- r_e, r_d = growth rates
- m_{ee}, m_{dd} intra-morph competition, m_{ed}, m_{de} inter-morph competition
- μ = small positive constant, measuring amount of mutation
- d, e = positive constants, allow mutation to affect morphs differently

Competition-diffusion-mutation model

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- terminology: interested in trade-off between dispersal and growth

$$D_d > D_e, \quad r_e > r_d$$

$\Rightarrow \quad n_e =$ density of establisher, $\quad n_d =$ density of disperser

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- motivation: evidence that in some species, more dispersive individuals are less fecund, so have lower growth rate *e.g.*, speckled wood butterfly

[Hughes, Hill and Dytham, Proc. Roy. Soc. London Ser. B (2003)]

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Question: how does mutation (μ) between phenotypes affect the invasion of the species into a region where it was previously absent?

In particular, the speed of invasion?

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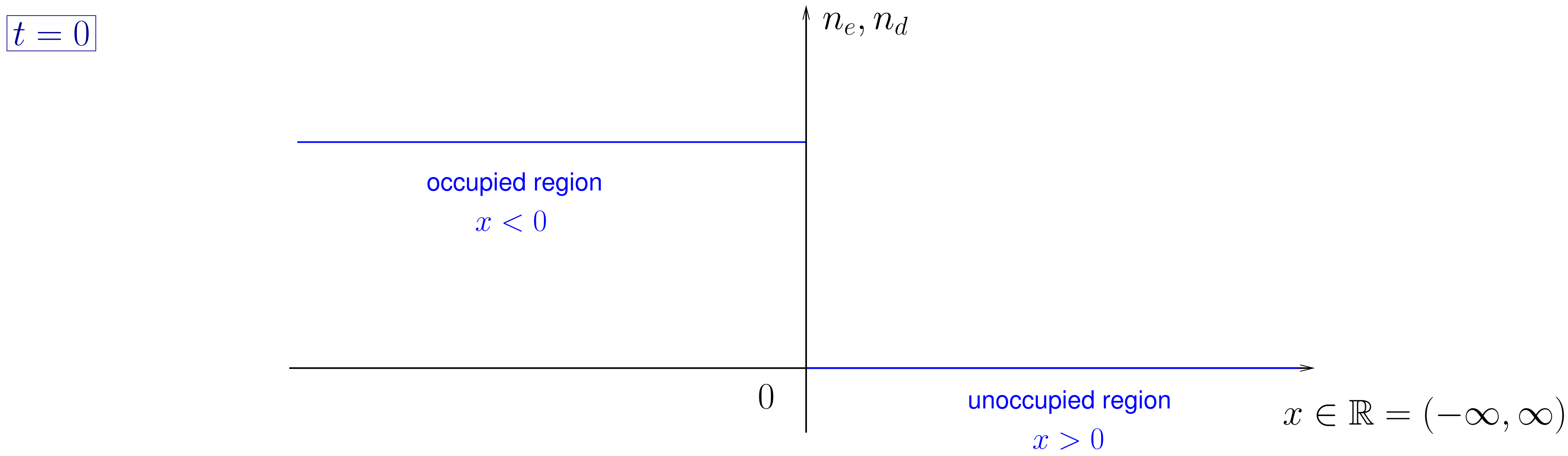
- mathematically: if both n_e, n_d initially have initial condition



what happens as t increases, and how is this affected by μ?

Some notation

- set

$$u = \begin{pmatrix} n_e \\ n_d \end{pmatrix} \in \mathbb{R}^2, \quad A = \text{diag}(D_e, D_d),$$

$$f(n_e, n_d) = \begin{pmatrix} r_e n_e (1 - m_{ee} n_e - m_{ed} n_d) - \mu e\, n_e + \mu d\, n_d \\ r_d n_d (1 - m_{de} n_e - m_{dd} n_d) + \mu e\, n_e - \mu d\, n_d \end{pmatrix}.$$

so that system becomes

$$u_t = A u_{xx} + f(u)$$

- for later, write

$$g(n_e, n_d) = \begin{pmatrix} r_e n_e (1 - m_{ee} n_e - m_{ed} n_d) \\ r_d n_d (1 - m_{de} n_e - m_{dd} n_d) \end{pmatrix}, \quad M = \begin{pmatrix} -e & d \\ e & -d \end{pmatrix},$$

and hence

$$f(u) = g(u) + \mu M u$$

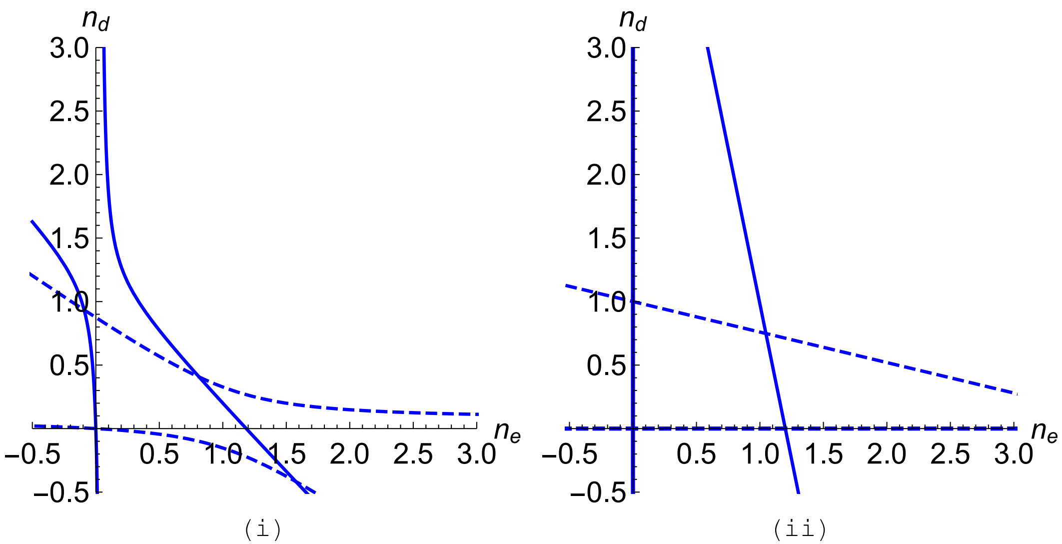
Assumptions and basic facts

(a) competition parameters: assume that

$$m_{ee} > m_{ed}, \quad m_{dd} > m_{de}$$

i.e. intra-morph competition is larger than inter-morph competition

(b) equilibria: for small mutation μ, there is an unstable extinction equilibrium $(0, 0)$, and a stable co-existence equilibrium (n_e^*, n_d^*) ('monostable')



Example of nullclines for (i) $\mu > 0$ (ii) $\mu = 0$

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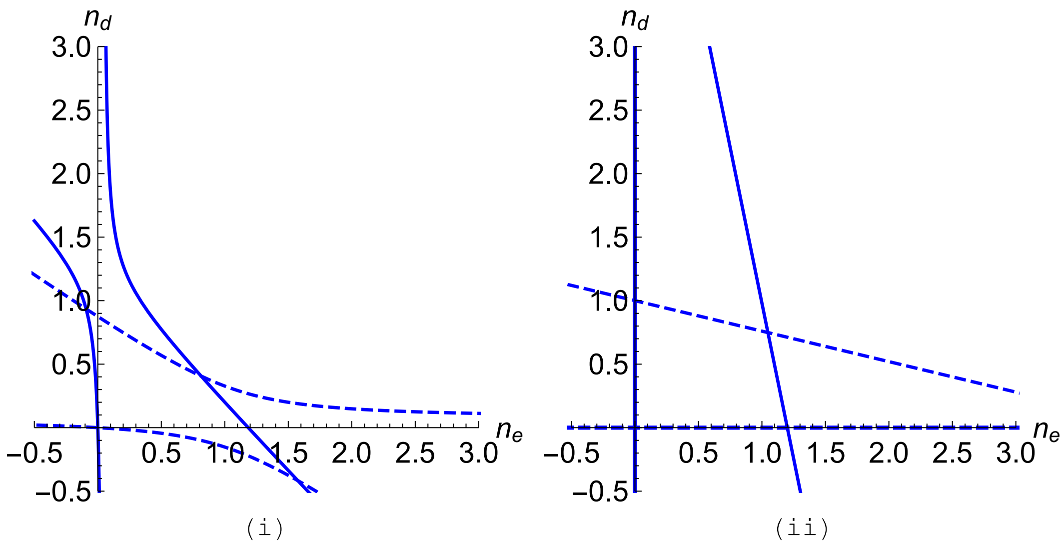

Example of nullclines for (i) $\mu > 0$ (ii) $\mu = 0$

- [Cantrell, Cosner+Yu, J. Biol. Dynamics, online March 2018]:
  - detailed study of equilibria/phase plane for various parameter regimes

(c) Jacobian and co-operativity - the interaction term

$$f(n_e, n_d) = \begin{pmatrix} r_e n_e(1 - m_{ee}n_e - m_{ed}n_d) - \mu e\, n_e + \mu d\, n_d \\ r_d n_d(1 - m_{de}n_e - m_{dd}n_d) + \mu e\, n_e - \mu d\, n_d \end{pmatrix}.$$

has Jacobian

$$f'(n_e, n_d) = \begin{pmatrix} r_e(1 - 2m_{ee}n_e - m_{ed}n_d) - \mu e & \mu d - r_e m_{ed} n_e \\ \mu e - r_d m_{de} n_d & r_d(1 - m_{de}n_e - 2m_{dd}n_d) - \mu d \end{pmatrix}$$

- so when mutation $\mu > 0$, off-diagonal elements of $f'(n_e, n_d)$ are positive when n_e, n_d are small but not in general

$\therefore$ system is not co-operative in general, but has co-operative structure close to $(0, 0)$

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- contrast: when $\mu = 0$, not co-operative for any densities n_e, n_d, but becomes co-operative under change of variables $n_d \to$ constant $- n_d$

(c) Jacobian and co-operativity.....ctd

- background: if f is co-operative, that is

$$\frac{\partial f_i}{\partial u_j}(u) \geq 0 \text{ whenever } i \neq j,$$

then the system

$$u_t = Au_{xx} + f(u)$$

is order preserving:

if $u, \hat{u} : \mathbb{R} \to \mathbb{R}^2$ are bounded and such that

$$u(x,0) \leq \hat{u}(x,0) \quad \text{for all} \quad x \in \mathbb{R},$$

and

$$u_t \leq Au_{xx} + f(u), \qquad \hat{u}_t \geq A\hat{u}_{xx} + f(\hat{u}) \quad \text{for all } (x,t) \in \mathbb{R} \times (0,\infty),$$

then

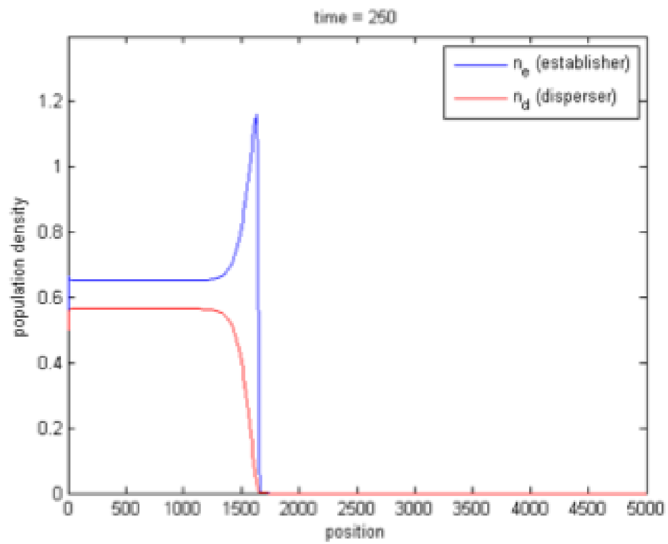
$$u(x,t) \leq \hat{u}(x,t) \quad \text{for all} \quad (x,t) \in \mathbb{R} \times [0,\infty)$$

Motivating previous work

- model was introduced by Elliott and Cornell, Dispersal Polymorphism and the Speed of Biological Invasions, PLOS One, 2012
- numerical simulation and linear analysis around $(0,0)$
- when mutation $\mu > 0$, found numerical evidence that given Heaviside initial conditions of the form

$$n_e(x,0), n_d(x,0) = \begin{cases} \text{positive constant} & \text{if } x < 0 \\ 0 & \text{if } x > 0 \end{cases},$$

  the two morphs n_e, n_d spread into the state $(0,0)$ at a single speed



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- used method of van Saarloos, Phys Rpts, 2003 (dispersion relation, stationary phase approximation) to argue that in the limit when $\mu \to 0$, there are three possible spreading speeds

$$v_d = 2\sqrt{D_d\, r_d}, \quad v_e = 2\sqrt{D_e\, r_e}, \quad v_a = \frac{r_e D_d - r_d D_e}{\sqrt{(r_e - r_d)(D_d - D_e)}}$$

- argued that speed v_a, which
  - is larger than v_e, v_d
  - depends on both sets of dispersal and growth parameters

  is admissible/selected provided

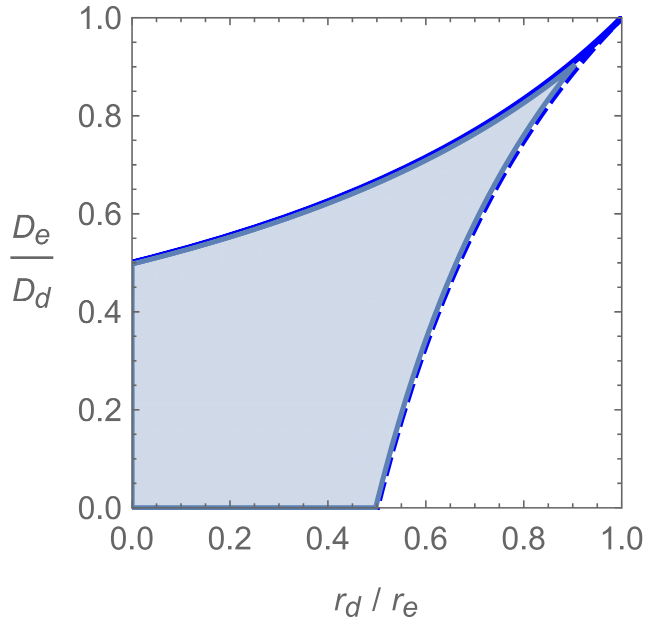
$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \quad \text{and} \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2$$

• predicted that in the parameter region Λ, where both

$$D_d > D_e, \quad r_e > r_d$$

and

$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \quad \text{and} \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2,$$



then when there is a small positive mutation $\mu > 0$, the 2 morphs spread together at faster speed than either would spread in isolation

'anomalous spreading'

Other related work

- Cane-toad models

$$u_t = \theta u_{xx} + \alpha u_{\theta\theta} + r\left(1 - \int_{\theta_{\min}}^{\theta_{\max}} u\, d\theta\right)$$

$$u(x,t,\theta) = \text{ density of toads of trait } \theta, \quad u_\theta(x,t,\theta_{\min}) = u_\theta(x,t,\theta_{\max}) = 0$$

e.g.

- Bénichou, Calvez, Meunier and Voituriez, Phys. Rev. E, 2012; Bouin, Calvez, Meunier, Mirrahimi, Perthame, CRAS, 2012; Bouin + Calvez, Nonlinearity, 2014; O. Turanova, M3AS, 2015; Bouin + Henderson, 2017; Bouin, Henderson + Ryzhik, J. Maths Pures Appl., Quart. Appl. Math., 2017, ...

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- Griette + Raoul, JDE 2016

  – study existence $+$ properties/shape of travelling waves when $D_d = D_e, \quad d = e$

  - exploit $D_e = D_d$ to study profiles, get explicit formula for minimal wave speed

- Girardin, Nonlinearity, 2018; M3AS 2018

  - general results on spreading speeds/travelling waves for N morphs; linear determinacy

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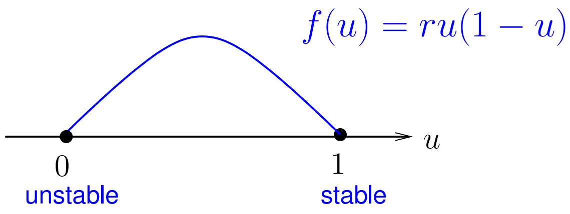
- Tang and Fife, ARMA 1980

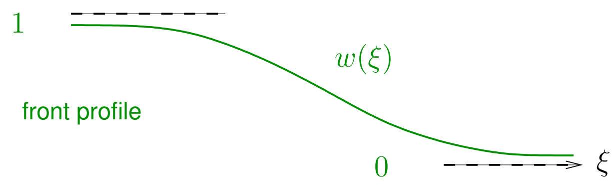
  - $\mu = 0$, existence of travelling waves for all speeds $\geq \max\{2\sqrt{D_d\, r_d}, 2\sqrt{D_e\, r_e}\}$

Prototype 'monostable' problem: for the Fisher-KPP equation

$$u_t = du_{xx} + ru(1-u)$$



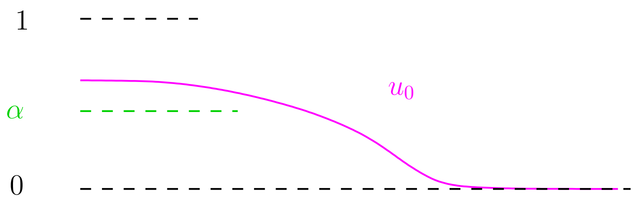
• (Fisher, KPP '37) there exist decreasing travelling front solutions $u(x,t) = w(x - ct)$



for all speeds

$$c \geq c^*$$

• (Aronson-Weinberger '78) the minimal front speed c^* can be characterised as a spreading speed: for an initial condition $u(x,0) = u_0(x)$ of form



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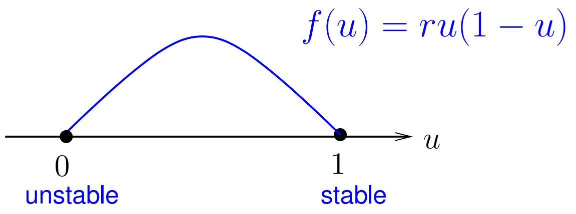

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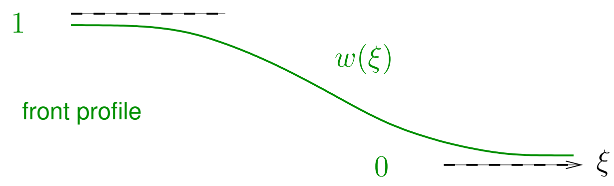

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$$c \geq c^* \; = \boxed{2\sqrt{dr} \quad \text{linear speed}}$$

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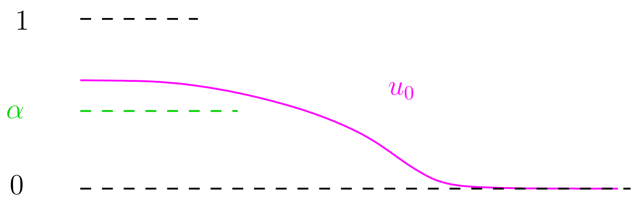

the solution u of $u_t = du_{xx} + f(u)$ 'spreads' to the right at speed c^*

1. The Linearised Problem at $(0, 0)$: What is it, and does it determine the speed of spread?

The linearised problem about $(0,0)$

- linearised PDE system

$$u_t = Au_{xx} + f'(0)u$$

where

$$f'(0) = \begin{pmatrix} r_e - \mu e & \mu d \\ \mu e & r_d - \mu d \end{pmatrix}$$ has positive off-diagonal elements

- substituting travelling-wave ansatz $u(x,t) = e^{-\beta(x-ct)}q$, where $q \in \mathbb{R}^2$ is positive vector, gives

$$\left(\beta A + \beta^{-1} f'(0)\right) q = cq$$

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- so for given $\beta > 0$, the speed c is the Perron-Frobenius eigenvalue of $H_{\beta,\mu} := \beta A + \beta^{-1} f'(0) = \beta A + \beta^{-1}(g'(0) + \mu M)$, *i.e.*

$$c = \eta_{PF}(H_{\beta,\mu}),$$

and $q > 0$ is the corresponding eigenvector, which is positive

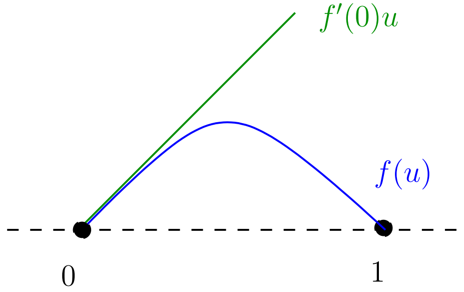
- minimising $\eta_{PF}(H_{\beta,\mu})$ over β gives the minimal c with a positive vector q: define the μ-dependent linear value

$$c(\mu) = \min_{\beta>0} \eta_{PF}(H_{\beta,\mu})$$

Linear determinacy: do solutions spread at the linear speed $c(\mu)$?

• famous <u>sufficient</u> condition for linear determinacy for the scalar equation $u_t = du_{xx} + f(u)$

$$f(u) \le f'(0)u \quad \text{for all} \quad u \in (0,1)$$



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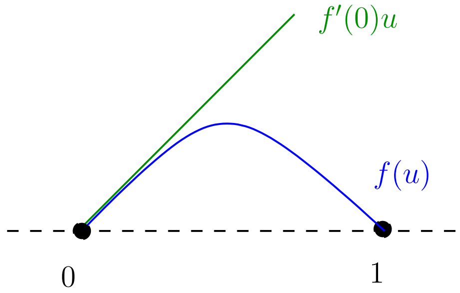

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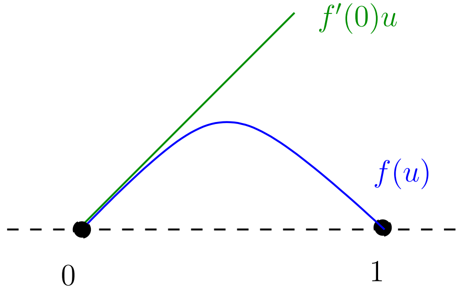

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- Here, when μ is small,

yes, linearly determinate +

spreading speed = minimal travelling-wave speed

- [Morris et al, arXiv:1612.06768 [math.AP]]: if m_{ed}, m_{de} small
- exploit 'trapping framework' of [Wang, J. Nonlinear Science (2011)]

$f^-(u) \leq f(u) \leq f^+(u)$, where f^-, f^+ are co-operative, $(f^-)'(0) = f'(0) = (f^+)'(0)$

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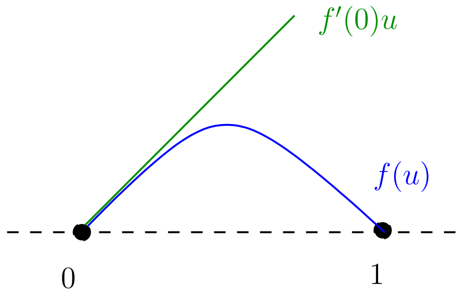

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- [Morris et al, arXiv:1612.06768 [math.AP]]: if m_{ed}, m_{de} small
- [Girardin, Nonlinearity 2018]: if $\eta_{PF}(f'(0)) > 0$

2. Exploiting the Linearised Problem:

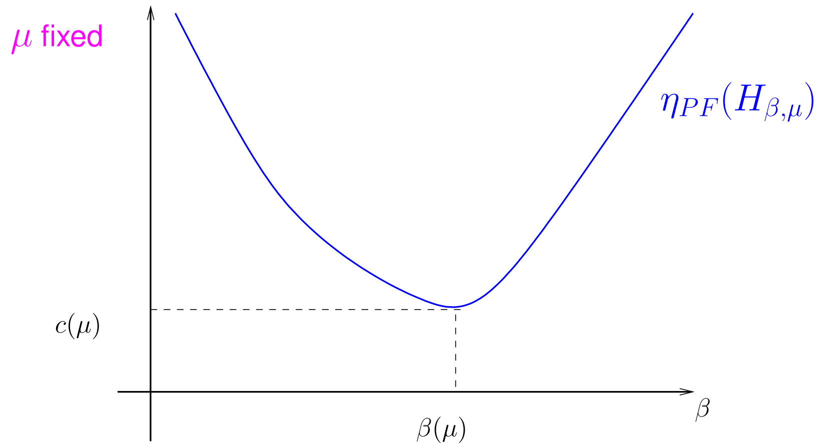
how does the
(linearised) spreading speed $c(\mu)$ depend
on the mutation rate μ?

Terminology: (linearised) spreading speed is given by

$$c(\mu) = \min_{\beta>0} \eta_{PF}(H_{\beta,\mu}) = \eta_{PF}(H_{\beta(\mu),\mu})$$

where

$$H_{\beta,\mu} = \beta \text{ diag}(D_e, D_d) + \beta^{-1}(\text{diag}(r_e, r_d) + \mu M)$$



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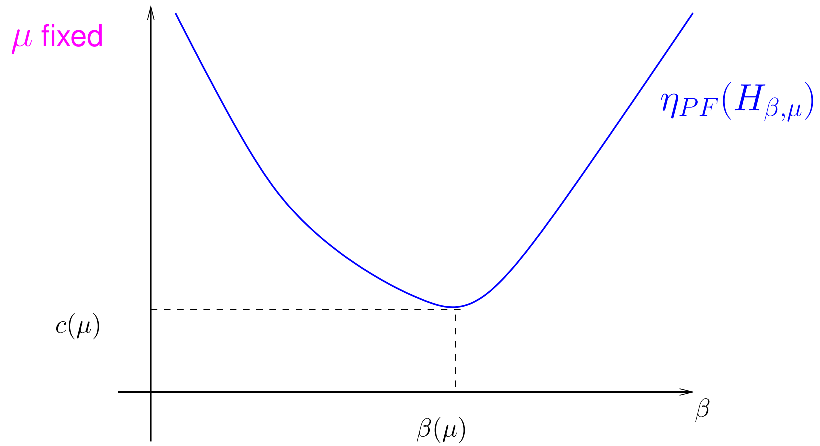

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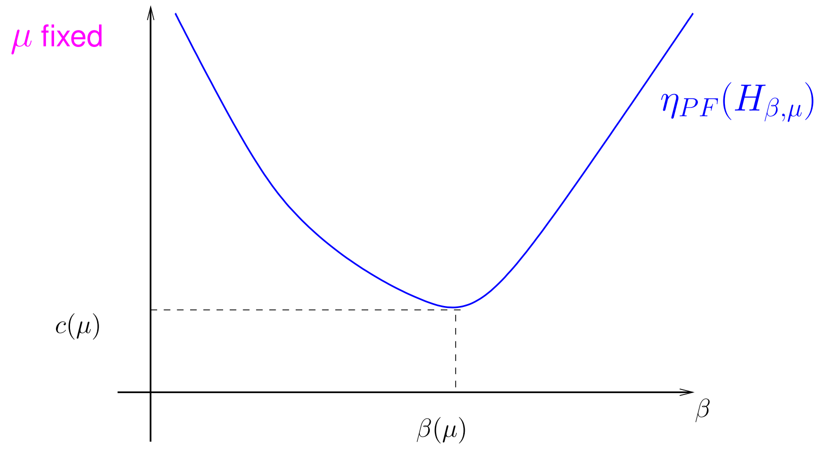

$c(\mu)$ is a non-increasing function of μ

$\therefore$ increasing mutation slows down the rate of spread

cf. [Altenberg, PNAS (2012)]: positive semigroup framework

reduction phenomenon - greater mixing $\Rightarrow$ lowered growth

- the proof exploits properties of the Perron-Frobenius eigenvalue η_{PF}:

(i) convexity properties of η_{PF}:

> (Cohen, '81) if P_1, P_2 are diagonal and Q has positive off-diagonal elements, then for $0 < \alpha < 1$,
>
> $$\eta_{PF}(\alpha P_1 + (1-\alpha)P_2 + Q) \leq \alpha \eta_{PF}(P_1 + Q) + (1-\alpha)\eta_{PF}(P_2 + Q)$$

(ii) the fact that $\eta_{PF}(M) = 0$: since $M = \begin{pmatrix} -e & d \\ e & -d \end{pmatrix}$ has zero column sums, we have

$$(1 \quad 1)\begin{pmatrix} -e & d \\ e & -d \end{pmatrix} = (0 \quad 0)$$

Idea of the proof ....

Step 1: take $\mu > \mu_0$, and define diagonal matrices

$$P := \beta(\mu_0)\left[\beta(\mu_0)\text{diag}(D_e, D_d) + \beta(\mu_0)^{-1}\text{diag}(r_e, r_d) - c(\mu_0)I\right], \quad Z = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$$

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$$\begin{aligned} \eta_{PF}\left(\frac{1}{\mu}P + M\right) &\leq \frac{\mu_0}{\mu}\eta_{PF}\left(\frac{1}{\mu_0}P + M\right) + \left(1 - \frac{\mu_0}{\mu}\right)\eta_{PF}(Z + M) \\ &= \frac{\mu_0}{\mu}\eta_{PF}\left(\frac{1}{\mu_0}P + M\right) + \left(1 - \frac{\mu_0}{\mu}\right)\eta_{PF}(M) = 0 \end{aligned}$$

because

$$\eta_{PF}(M) = 0 \quad \text{and} \quad \eta_{PF}\left(\frac{1}{\mu_0}P + M\right) = \frac{1}{\mu_0}\eta_{PF}(P + \mu_0 M) = 0$$

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Step 3:

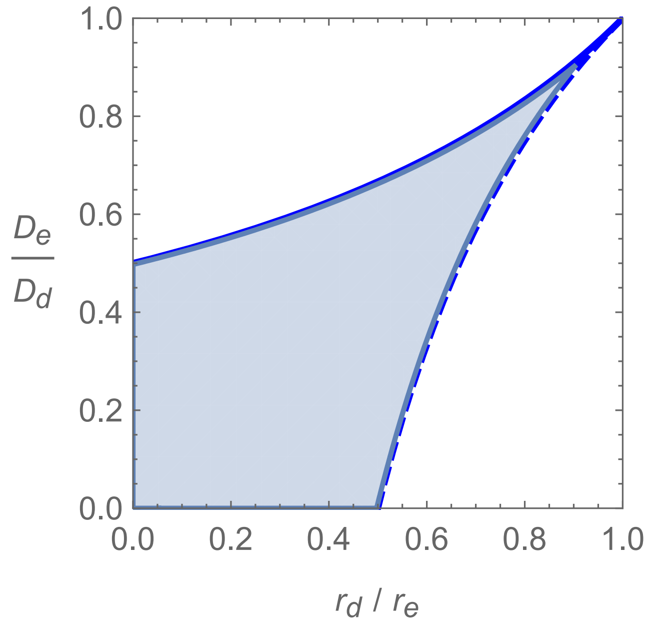
$$\eta_{PF}\left(\beta(\mu_0)\text{diag}(D_e, D_d) + \beta(\mu_0)^{-1}(\text{diag}(r_e, r_d) + \mu M)\right) \leq c(\mu_0)$$

$$\therefore \quad c(\mu) := \min_{\beta>0} \eta_{PF}\left(\beta\text{diag}(D_e, D_d) + \beta^{-1}(\text{diag}(r_e, r_d) + \mu M)\right) \leq c(\mu_0)$$

3. Exploiting the Linearised Problem:

understanding the 'anomalous spreading' condition

$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2, \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2$$



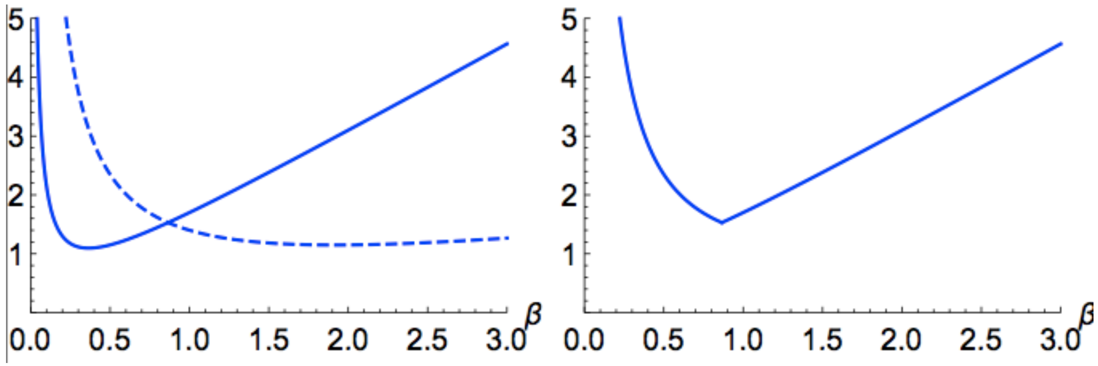
Linearisation when $\mu = 0$ and 'anomalous spreading' condition

- when mutation $\mu = 0$, the matrix

$$H_{\beta,0} = \text{diag}(\beta D_e + \beta^{-1} r_e, \beta D_d + \beta^{-1} r_d)$$

  is diagonal, so has no 'Perron-Frobenius' eigenvalue

- consider larger of the two eigenvalues $\beta D_e + \beta^{-1} r_e$ and $\beta D_d + \beta^{-1} r_d$ for each β *e.g.*



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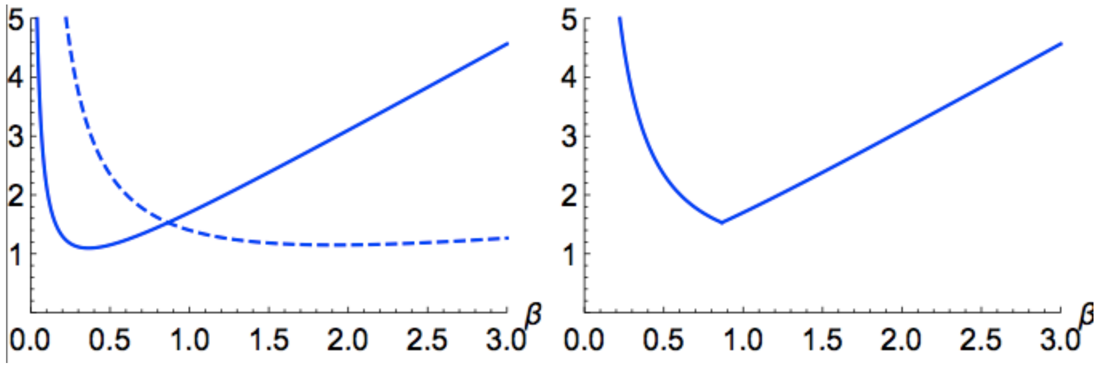


- if $D_d > D_e$ and $r_e > r_d$, the curves cross at a value β^* between the minima of the 2curves, so $\min_{\beta>0}$ of max of the 2 eigenvalues is attained where curves cross, if

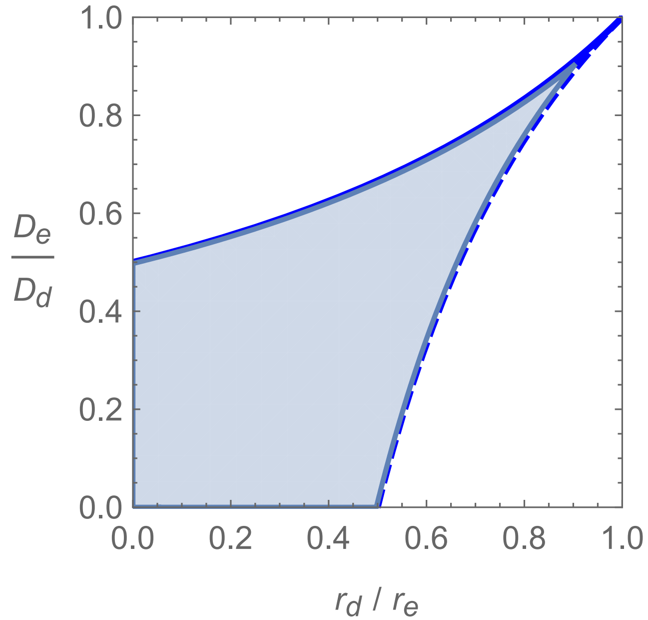
$$\boxed{\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \quad \text{and} \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2}$$

  i.e. condition for the 2 morphs to spread together at a speed faster than either spreads alone

4. Exploiting the Linearised Problem:

convergence of $c(\mu)$ and the ratio of the phenotypes in the leading edge as $\mu \to 0$ in the 'anomalous spreading' region Λ

$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2, \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2$$



- when $\mu > 0$, minimal speed front of linearised problem has form

$$u(x,t) = e^{-\beta(\mu)(x-c(\mu)t)}q$$

where $q = (q_e \;\; q_d)^T$ is a Perron-Frobenius eigenvector of

$$H_{\beta(\mu),\mu} = \beta(\mu)A + \beta(\mu)^{-1}(g'(0) + \mu M)$$

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$$\boxed{\beta(\mu) \to \beta^* := \sqrt{\frac{r_e - r_d}{D_d - D_e}}, \quad c(\mu) \to c_0 := \frac{r_e D_d - r_d D_e}{\sqrt{(r_e - r_d)(D_d - D_e)}}}$$

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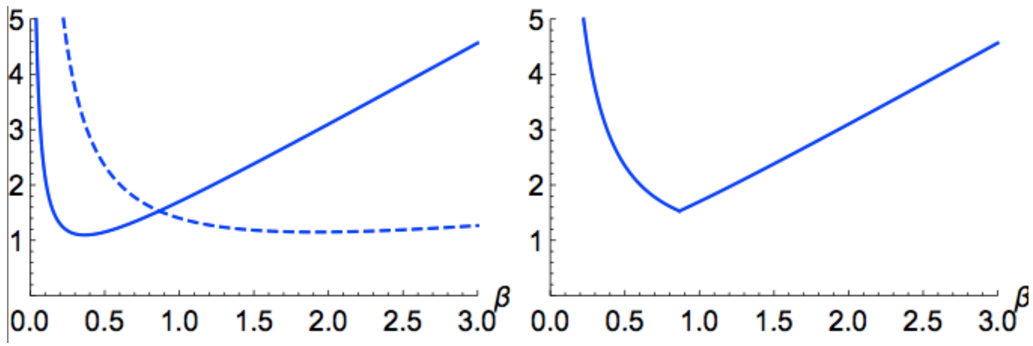
and the matrix

$$H_{\beta^*,0} = \text{diag}(c_0, c_0)$$

has a two-dimensional eigenspace



What happens to the principal eigenvector q as $\mu \to 0$?

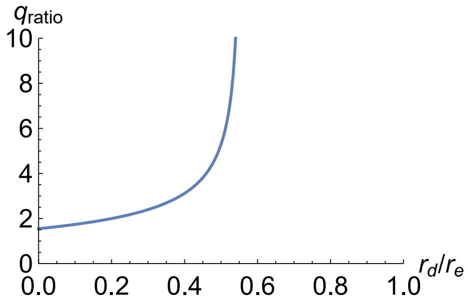
• provided $c(\mu)$, etc, differentiable and the limits $\lim_{\mu\to 0} \frac{c(\mu)-c_0}{\mu}$ and $\lim_{\mu\to 0} \frac{\beta(\mu)-\beta^*}{\mu}$ exist,

$$q_{\text{ratio}} = \frac{q_d}{q_e} \to \sqrt{\left(\frac{2D - rD - 1}{2r - rD - 1}\right) m} \quad \text{as} \quad \mu \to 0,$$

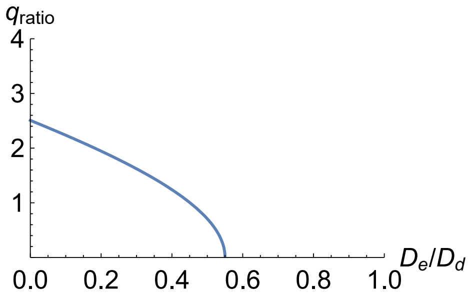
where

$$m := \frac{e}{d}, \quad D := \frac{D_e}{D_d}, \quad r := \frac{r_d}{r_e}$$

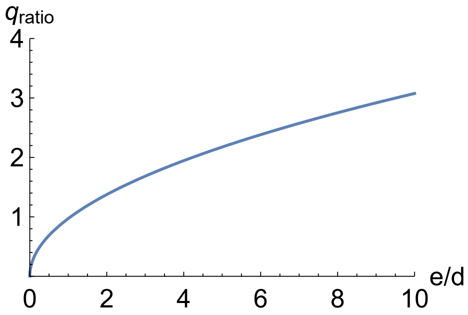
e.g.



(i)



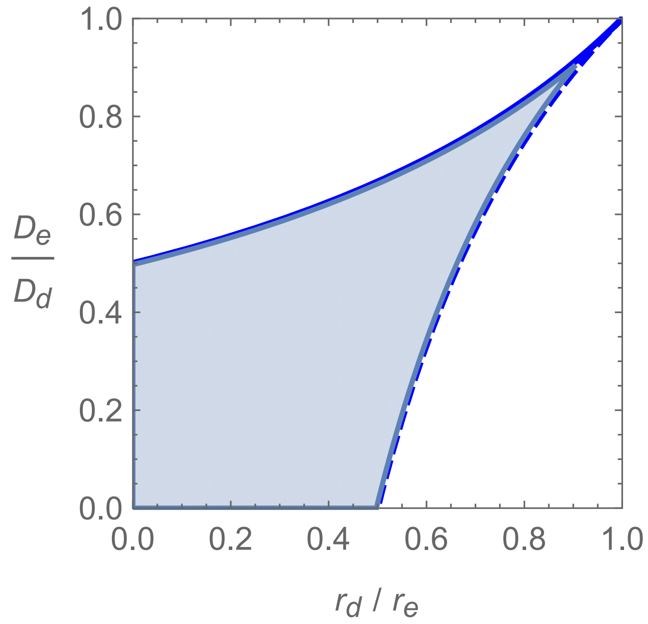
(ii)



(iii)

where D and m are fixed in (i), r and m in (ii), and r and D in (iii)

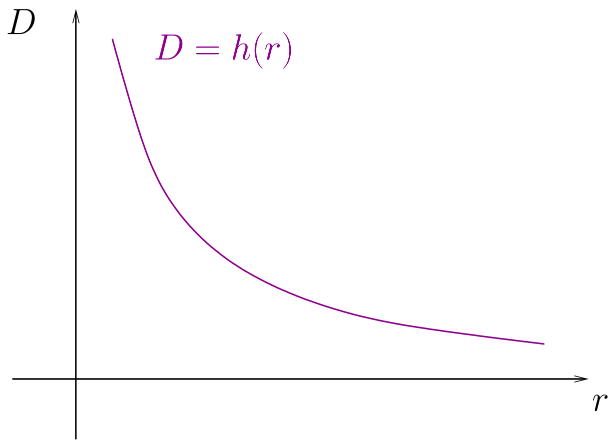
5. Trade-offs and the ‘anomalous spreading’ region



- suppose a functional form of trade off between dispersal and growth, say

$$D = h(r)$$

where $h : (0, \infty) \to (0, \infty)$ is decreasing



- are the 'anomalous spreading' conditions

$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \quad \text{and} \quad \frac{D_d}{D_e} + \frac{r_d}{r_e} > 2$$

satisfied for a given trade-off function h?

- inversely-proportional case: conditions always hold when

$$h(r) = \frac{K}{r}, \qquad K \text{ constant}$$

since

$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \iff \frac{r_d}{r_e} + \frac{r_e}{r_d} > 2 \iff (r_d - r_e)^2 > 0$$

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since

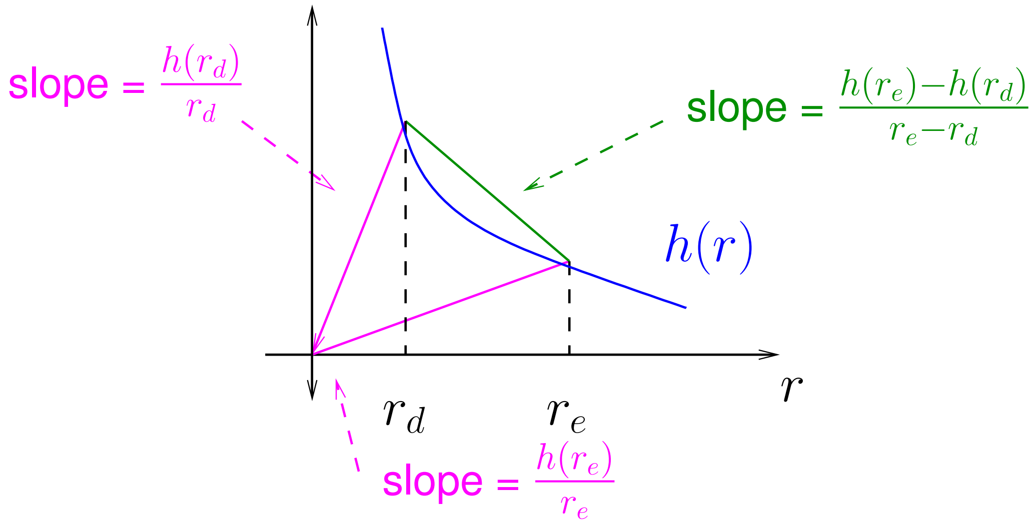
$$\frac{D_e}{D_d} + \frac{r_e}{r_d} > 2 \;\Leftrightarrow\; \frac{r_d}{r_e} + \frac{r_e}{r_d} > 2 \;\Leftrightarrow\; (r_d - r_e)^2 > 0$$

- geometric condition for general case: if $r_e > r_d$, then

$$\frac{h(r_e)}{h(r_d)} + \frac{r_e}{r_d} > 2 \quad \text{and} \quad \frac{h(r_d)}{h(r_e)} + \frac{r_d}{r_e} > 2$$

if and only if

$$\frac{h(r_e)}{r_e} < -\left(\frac{h(r_e)-h(r_d)}{r_e-r_d}\right) < \frac{h(r_d)}{r_d}$$



More open questions

- more information about the shape of the travelling waves?
  - in particular, what happens at the back of the front?
- anomalous spreading for more than 2 species?
  - some recent work of Cornell and Keenan on multi-species case
- other ways of modelling mutation?

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arXiv:1612.06768 [math.AP]

Thank you for your attention.....