The retreat of the less fit allele in a population-controlled model for population genetics

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Classical model for 1-locus diploid species with alleles a and A:

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{aa} = \frac{r[2\rho_{aa}+\rho_{aA}]^2}{4[\rho_{aa}+\rho_{aA}+\rho_{AA}]} - \tau_{aa}\rho_{aa}$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{aA} = \frac{2r[2\rho_{aa}+\rho_{aA}][2\rho_{AA}+\rho_{aA}]}{4[\rho_{aa}+\rho_{aA}+\rho_{AA}]} - \tau_{aA}\rho_{aA}$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{AA} = \frac{r[2\rho_{AA}+\rho_{aA}]^2}{4[\rho_{aa}+\rho_{aA}+\rho_{AA}]} - \tau_{AA}\rho_{AA}.$$

Heterozygote intermediate:

$$\tau_{AA} < \tau_{aA} < \tau_{aa}$$

Souplet and Winkler (2011, 2012) showed that

$$\lim_{t\to\infty} \frac{2\rho_{AA}(x,t) + \rho_{aA}}{2[\rho_{aa} + \rho_{aA} + \rho_{AA}]} = 1,$$

uniformly on bounded sets. The proof relies on showing that all the densities approach infinity, but ρ_{AA} does so more quickly. (Unrealistic model.)

$$\left\{ \frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2} \right\} \rho_{aa} = \frac{R(\rho)[2\rho_{aa} + \rho_{aA}]^2}{4[\rho_{aa} + \rho_{aA} + \rho_{AA}]} - \tau_{aa}\rho_{aa}$$

$$\left\{ \frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2} \right\} \rho_{aA} = 2\frac{R(\rho)[2\rho_{aa} + \rho_{aA}][2\rho_{AA} + \rho_{aA}]}{4[\rho_{aa} + \rho_{aA} + \rho_{AA}]} - \tau_{aA}\rho_{aA}$$

$$\left\{ \frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2} \right\} \rho_{AA} = \frac{R(\rho)[2\rho_{AA} + \rho_{aA}]^2}{4[\rho_{aa} + \rho_{aA} + \rho_{AA}]} - \tau_{AA}\rho_{AA},$$

where

$$\rho := \rho_{aa} + \rho_{aA} + \rho_{AA}.$$

MAIN THEOREM.
Let the death rates satisfy the inequalities

$$\frac{1}{2}[\tau_{aa} + \tau_{AA}] \leq \tau_{aA} < \tau_{aa}$$

Let the function $R(\rho)$ satisfy the following conditions.

i. There are numbers $\ell < k < m$ such that when $\ell \leq \rho \leq m$, $R(\rho)$ is nonnegative and continuously differentiable, and $R'(\rho) < 0$

ii. $R(\ell) = \tau_{aa},\ R(k) = \tau_{aA}$, and $R(m) = \tau_{AA}$. In particular, $(\ell, 0, 0)$ and $(0, 0, m)$ are equilibria.

iii. $3\ell < k$.

Suppose that

$$\ell \leq \rho_{aa}(x,0) + \rho_{aA}(x,0) + \rho_{AA}(x,0) \leq m,$$

$$2\rho_{AA}(x,0) + \rho_{aA}(x,0) > 0 \text{ on some open set,}$$

and

$$\limsup_{|x|\to\infty}[\rho_{aa}(x,0) - \rho_{AA}(x,0)] \leq \ell.$$

Then for any c with $c < 2\sqrt{D[\tau_{aa} - \tau_{aA}]}$

$$\lim_{t\to\infty}[\max_{|x|\leq ct} \rho_{aa}(x,t)] = \lim_{t\to\infty}[\max_{|x|\leq ct} \rho_{aA}(x,t)]$$
$$= \lim_{t\to\infty}[\max_{|x|\leq ct} |m - \rho_{AA}(x,t)|] = 0.$$

Proofs

Let

$$h := \frac{\rho_{aA}^2 - 4\rho_{aa}\rho_{AA}}{4\rho}.$$

Equations become

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{aa} = [R(\rho) - \tau_{aa}]\rho_{aa} + R(\rho)h$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{aA} = [R(\rho) - \tau_{aA}]\rho_{aA} - 2R(\rho)h$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}\rho_{AA} = [R(\rho) - \tau_{AA}]\rho_{AA} + R(\rho)h.$$

$$\rho := \rho_{aa} + \rho_{aA} + \rho_{AA}$$

$$[R(\rho) - \tau_{aa}]\rho \le \left\{ \frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2} \right\} \rho \le [R(\rho) - \tau_{AA}]\rho.$$

$$\ell \le \rho(x, 0) \le m \implies \ell \le \rho(x, t) \le m.$$

$$h := \frac{\rho_{aA}^2 - 4\rho_{aa}\rho_{AA}}{4\rho}.$$

$$\left\{\frac{\partial}{\partial t} - D\Delta\right\} h = -2\rho\,|\nabla\{[2\rho_{AA} + \rho_{aA}]/[2\rho]\}|^2$$
$$- [2\tau_{aA} - \tau_{aa} - \tau_{AA}]\rho_{aA}^2/[4\rho]$$
$$- \{\tau_{AA} + [\tau_{aa} - \tau_{aA}][\rho_{aA}/\rho] + [\tau_{aa} - \tau_{AA}][\rho_{AA}/\rho]\}h.$$

Let

$$\hat{h} := m^2 e^{-\tau_{AA} t}/[4\ell].$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} \hat{h} = -\tau_{AA}\hat{h}$$
$$\geq -\{\tau_{AA} + [\tau_{aa} - \tau_{aA}][\rho_{aA}/\rho] + [\tau_{aa} - \tau_{AA}][\rho_{AA}/\rho]\}\hat{h}.$$

$$h(x,t) \leq m^2 e^{-\tau_{AA} t}/[4\ell].$$

$$z := \rho_{aa} - \rho_{AA}$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} z$$

$$= -[\tau_{aa} - R(\rho)]\rho_{aa} - [R(\rho) - \tau_{AA}]\rho_{AA} \leq 0.$$

Then for any $\eta > 0$, $z \leq \hat{z}$, where

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} \hat{z} = 0$$

$$\hat{z}(x,0) = \ell + \eta + \max\{z(x,0) - \ell - \eta,\ 0\}.$$

$$\limsup_{t\to\infty}[\sup_x z(x,t)] \leq \ell.$$

$$q := 2\rho_{AA} + \rho_{aA}$$

$$\rho = q + z \le q + \ell + \eta \text{ when } t \text{ is large.}$$

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} q \ge [R(q + \ell + \eta) - \tau_{aA}]q$$

Then $q \ge \hat{q}$, where

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} \hat{q} = [R(\hat{q} + \ell + \eta) - \tau_{aA}]\hat{q}$$

$$\hat{q}(x, 0) = \min\{q(x, 0), [k - \ell - \eta]/2\}.$$

Monostable Fisher-KPP equation with slope $R(\ell + \eta) - \tau_{aA}$ at 0, and stable equilibrium $k - \ell - \eta$. If $c < 2\sqrt{D[\tau_{aa} - \tau_{aA}]}$, then

$$\liminf_{t\to\infty}[\min_{|x|\le ct} q(x, t)] \ge k - \ell.$$

Assume

$$R(3\ell) > \tau_{aA}, \text{ so that } k > 3\ell.$$

Then

$$\lim_{t\to\infty}[\sup_{|x|\leq ct} \rho_{aa}(x,t)] = 0.$$

Proof.

Apply previous result with c replaced by $\tilde{c}$ such that

$$c < \tilde{c} < 2\sqrt{D[\tau_{aa} - \tau_{aA}]}.$$

Choose

$$\eta < k - 3\ell.$$

Then $\rho \geq \frac{1}{2}q \geq \frac{1}{2}[k - \ell - \eta] > \ell$, so that $\nu := \tau_{aa} - R(\frac{1}{2}[k - \ell - \eta]) > 0$ for $|x| \leq \tilde{c}t,\ t$ large.

Then

$$\begin{aligned} \left\{ \frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2} \right\} \rho_{aa} &= [R(\rho) - \tau_{aa}]\rho_{aa} + R(\rho)h \\ &\leq -\nu\rho_{aa} + Ke^{-\tau_{AA}t} \end{aligned}$$

for $|x| \leq \tilde{c}t$ and t sufficiently large

Comparison function: Choose $\mu > 0$ so that

$$c < \frac{\nu - D\mu^2}{\mu} < \tilde{c},$$

and define

$$\begin{aligned}\hat{v}(|x|, t) :=& \gamma e^{[-\nu + D\mu^2]t} \cosh \mu x \\ &+ [K/(\nu - \tau_{AA})][e^{-\tau_{AA} t} - e^{-\nu t}]\end{aligned}$$

This satisfies the equation

$$\left\{ \frac{\partial}{\partial t} - D \frac{\partial^2}{\partial x^2} \right\} \hat{v} = -\nu \hat{v} + K e^{-\tau_{AA} t}.$$

For large t

$$\hat{v}(\tilde{c}t, t) \sim \frac{1}{2}\gamma e^{[-\nu + D\mu^2 + \tilde{c}\mu]t} + [K/(\nu - \tau_{AA})][e^{-\tau_{AA}t} - e^{-\nu t}].$$

Since the exponent is positive, one can choose γ so that $\hat{v}(\tilde{c}t, t) \geq m \geq \rho_{aa}$ for large t. Then $\rho_{aa} \leq \hat{v}$.

On the other hand, $\hat{v}$ is increasing in $|x|$, so that $\rho_{aa}(x,t) \le \hat{v}(x,t) \le \hat{v}(ct,t)$ for $|x| \le ct$. But

$\hat{v}(ct,t) \sim \frac{1}{2}\gamma e^{[-\nu+D\mu^2+c\mu]t} + [K/(\nu-\tau_{AA})][e^{-\tau_{AA}t} - e^{-\nu t}]$.

The first exponent is negative. Let

$$\hat{\alpha} := \min\{-[-\nu + D\mu^2 + c\mu], \tau_{AA}\}.$$

Then there is an M_{aa} such that

$$\max_{|x|\le ct} \rho_{aa}(x,t)] \le M_{aa} e^{-\hat{\alpha}t} \text{ for } |x| \le ct.$$

$$\rho_{aA}^2 = \rho h + 4\rho_{AA}\rho_{aa}.$$

$$\rho_{AA} \leq \rho \leq m \text{ and } \hat{\alpha} \leq \tau_{AA},$$

so

$$\rho_{aA} \leq M_{aA} e^{-\frac{1}{2}\hat{\alpha}t} \text{ for} |x| \leq ct.$$

The previous two results show that if $\tilde{\nu}$ is a lower bound for $-R'(\rho)\ell$ on the interval $[\ell, m]$, there is a K such that

$$\begin{aligned}\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\}[m-\rho] \\ &= -R(\rho)\rho + \tau_{aa}\rho_{aa} + \tau_{aA}\rho_{aA} + \tau_{AA}\rho_{AA} \\ &\leq -[R(\rho) - R(m)]\rho + Ke^{-\frac{1}{2}\hat{\alpha}t} \\ &\leq -\tilde{\nu}[m-\rho] + Ke^{-\frac{1}{2}\hat{\alpha}t}.\end{aligned}$$

This is essentially the inequality satisfied by ρ_{aa}, but with ν replaced by $\tilde{\nu}$ and τ_{AA} replaced by $\frac{1}{2}\hat{\alpha}$.

$$\max_{|x|\leq ct}[m - \rho(x,t)] \leq Me^{-\bar{\alpha}t}.$$

$$\max_{|x|\leq ct}[m - \rho_{AA}] \leq M_{AA}e^{-\bar{\alpha}t}.$$

Speed limit:

Suppose that

$$q(x,0)e^{\sqrt{[\tau_{aa}-\tau_{AA}]/D}x} \leq \overline{M}.$$

Note that

$$\left\{\frac{\partial}{\partial t} - D\frac{\partial^2}{\partial x^2}\right\} q = Rq - 2\tau_{AA}\rho_{AA} - \tau_{aA}\rho_{aA}$$
$$\leq [\tau_{aa} - \tau_{AA}]q.$$

Comparison function:

$$\bar{q} := \overline{M}e^{-\sqrt{[\tau_{aa}-\tau_{AA}]/D}\{x-2\sqrt{D[\tau_{aa}-\tau_{AA}]}t\}}$$

Comparison principle: $q \leq \hat{q}$, so that if

$$c > 2\sqrt{D[\tau_{aa} - \tau_{AA}]},$$
$$\lim_{t\to\infty}[\max_{x>ct} q(x,t)] = 0.$$

Corresponding Fisher-KPP equation:

$$\left\{ \frac{\partial}{\partial t} - D\Delta \right\} U$$
$$= U(1 - U)[(\tau_{aa} - \tau_{aA})(1 - U) + (\tau_{aA} - \tau_{AA})U].$$

Spreading speed (Hadeler and Rothe, 1975)

$$c^* := \begin{cases} 2\sqrt{D[\tau_{aa} - \tau_{aA}]} \text{ when } \tau_{aa} - \tau_{aA} \geq \frac{1}{4}[\tau_{aa} - \tau_{AA}] \\ \frac{1}{2} D^{1/2}[\tau_{aa} - \tau_{AA}] \Big/ \sqrt{\frac{1}{2}[\tau_{aa} - \tau_{AA}] - [\tau_{aa} - \tau_{aA}]} \\ \qquad\qquad \text{when } \tau_{aa} - \tau_{aA} \leq \frac{1}{4}[\tau_{aa} - \tau_{AA}] \end{cases}$$