Interaction of clines under the prism of generalized travelling waves

Benoît Sarels

Sorbonne Université, Laboratoire Jacques-Louis Lions

Nonlinear waves and networks
INSA Rouen
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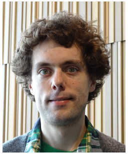
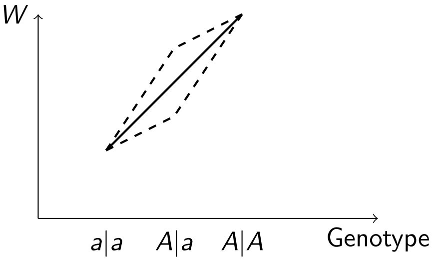
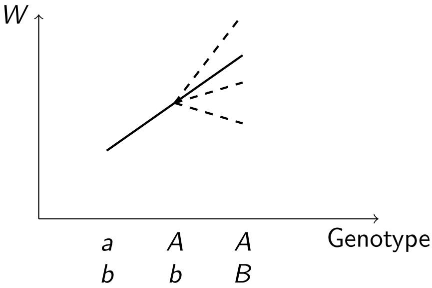
Population genetics systems with genetic incompatibilities


Joint work with : Matthieu Alfaro (Université de Rouen)
Quentin Griette (Université de Bordeaux)
Denis Roze (Marine Station Roscoff, CNRS).

- Genetic incompatibilities = non-linear interactions
- Dominance, epistasis





Population genetics equations and their solutions

Case study: two underdominant loci in diploid individuals

- Model establishment
- Numerical simulations
- Generalized travelling waves

Opening: N underdominant loci in diploid individuals

Population genetics equations and their solutions

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One locus, two alleles I

- Population in a linear habitat
- Diploid individuals
- Life cycle
  1. Random fusion of gametes $\rightarrow$ birth of new individuals
  2. Production of gametes (according to fitness)
  3. Migration of gametes
- p frequency of allele A
  $1 - p$ frequency of allele a
- W_{aa}, W_{Aa}, W_{AA} fitnesses of individuals

$$W_{aa} = 1$$
$$W_{Aa} = 1 + s_A$$
$$W_{AA} = 1 + 2s_A$$

with $0 \leq s_A$

$$W_{aa} = 1$$
$$W_{Aa} = 1 + s_A - S_A$$
$$W_{AA} = 1 + 2s_A$$

with $0 \leq s_A < S_A$ (underdominance)

One locus, two alleles II

1. Random fusion of gametes → birth of new individuals
   p^2 frequency of individuals AA, $\quad (1-p)^2$ frequency of individuals aa,
   $2p(1-p)$ frequency of individuals Aa
2. Production of gametes (according to fitness)

$$p' = \frac{(1+s_A)p(1-p) + (1+2s_A)p^2}{(1-p)^2 + 2(1+s_A)p(1-p) + (1+2s_a)p^2} \quad \text{or}$$
$$p' = \frac{(1+s_A-S_A)p(1-p) + (1+2s_A)p^2}{(1-p)^2 + 2(1+s_A-S_A)p(1-p) + (1+2s_a)p^2}$$

3. Migration of gametes

$$p''(x) = \int_{-\infty}^{+\infty} p'(x-\delta x) f(\delta x) d(\delta x)$$

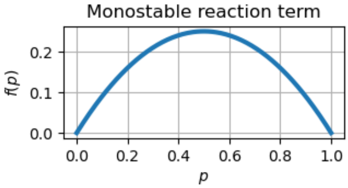
   where f has mean 0 and variance σ^2

- Discrete time process approximated through a continuous time process → equation on $p(x,t)$

Reaction-diffusion equations

Suppose $s_A \ll 1$, we get

$$\partial_t p = s_A p(1-p) + \frac{\sigma^2}{2}\partial_{xx}^2 p$$

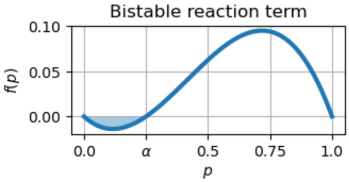


Suppose $s_A, S_A \ll 1$, we get

$$\partial_t p = \Big(s_A + S_A(2p-1)\Big)p(1-p) + \frac{\sigma^2}{2}\partial_{xx}^2 p$$

$$\partial_t p = 2S_A p(p-\alpha)(1-p) + \frac{\sigma^2}{2}\partial_{xx}^2 p$$

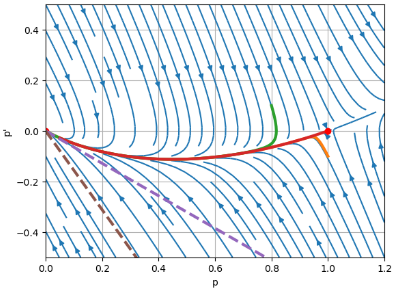
where $\alpha = \frac{S_A - s_A}{2S_A} > 0$



What do those equations have in common? What solutions are expected?

Their basic properties: common points

The monostable and the bistable equation have travelling wave solutions.



- Write the equation in abstract form

$$\partial_t p = f(p) + \partial^2_{xx} p$$

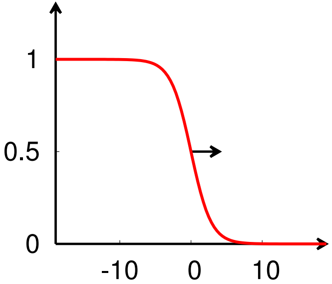
- Travelling wave

$$p(x,t) = \tilde{p}(z) \quad \text{with} \quad z = x - ct$$

- We search a couple $(c, \tilde{p})$ such that

$$-c\tilde{p}' = f(p) + \tilde{p}''$$

- Propagation of advantageous allele A



Their basic properties: differences

Monostable equation (logistic reaction term)

$$\partial_t p = s_A p(1-p) + \frac{\sigma^2}{2}\partial^2_{xx} p$$

- Continuum of possible speeds $c \geq 2\sigma\sqrt{s_A}$
- Fixed profile for a given speed
- No explicit solutions except (Ablowitz, 1978)

$$\tilde{p}(z) = \frac{1}{(1+\exp(z))^2}$$

for the speed $c = \frac{5}{\sqrt{6}}\sigma\sqrt{s_A}$

Bistable equation (cubic reaction term)

$$\partial_t p = 2S_A p(p-\alpha)(1-p) + \frac{\sigma^2}{2}\partial^2_{xx} p$$

- Unique speed $c = \frac{\sigma s_A}{\sqrt{S_A}}$
- Fixed profile
- Given explicitely by (Barton, 1979)

$$\tilde{p}(z) = \frac{1}{1+\exp(z)}$$

Population genetics equations and their solutions

Case study: two underdominant loci in diploid individuals

- Model establishment
- Numerical simulations
- Generalized travelling waves

Opening: N underdominant loci in diploid individuals

One more locus adds a layer of complexity

- Two loci, two alleles (same hypotheses as before)
  $q(x,t)$ frequency of allele B
  $1 - q(x,t)$ frequency of allele b
- W_{bb}, W_{Bb}, W_{BB} fitnesses of individuals

$$
\begin{aligned}
W_{bb} &= 1 \\
W_{Bb} &= 1 + s_B - S_B \\
W_{BB} &= 1 + 2s_B
\end{aligned}
$$

  with $s_B \geq 0$ and $S_B > s_B$
- $W_{x,y} = W_x W_y$

Two loci, two alleles I

- Possibility of recombination events during meiosis (recombination rate $0 < r \leq \frac{1}{2}$)
- Individual $\begin{array}{c|c} A & a \\ B & b \end{array}$ yields:

1. $\begin{array}{c} A \\ B \end{array}$ in proportion $\frac{1-r}{2}$
2. $\begin{array}{c} a \\ b \end{array}$ in proportion $\frac{1-r}{2}$
3. $\begin{array}{c} A \\ b \end{array}$ in proportion $\frac{r}{2}$
4. $\begin{array}{c} a \\ B \end{array}$ in proportion $\frac{r}{2}$

- y_1, y_2, y_3, y_4 frequencies of gametes AB, Ab, aB, ab (resp.)

1. Random fusion of gametes $\rightarrow$ birth of new individuals
   $z_{i,j}$ frequency of diploid individuals obtained through fusion of gametes i et j:
   $$z_{i,j} = \begin{cases} 2y_i y_j & \text{if} \quad i \neq j \\ y_i^2 & \text{if} \quad i = j \end{cases}$$

Two loci, two alleles II

2. Production of gametes (according to fitness)

$$z'_{i,j} = \frac{W_{i,j} z_{i,j}}{\bar{W}}$$

where $\bar{W} = \sum_{i,j} W_{i,j} z_{i,j}$.
We get

$$\begin{cases} y'_1 = z'_{1,1} + \frac{1}{2}(z'_{1,2} + z'_{1,3} + (1-r)z'_{1,4} + rz'_{2,3}) \\ y'_2 = z'_{2,2} + \frac{1}{2}(z'_{2,1} + z'_{2,4} + (1-r)z'_{2,3} + rz'_{1,4}) \\ y'_3 = z'_{3,3} + \frac{1}{2}(z'_{3,1} + z'_{3,4} + (1-r)z'_{3,2} + rz'_{1,4}) \\ y'_4 = z'_{4,4} + \frac{1}{2}(z'_{4,2} + z'_{4,3} + (1-r)z'_{4,1} + rz'_{2,3}) \end{cases}$$

Two loci, two alleles III

3. Migration of gametes

$$y''(x) = \int_{-\infty}^{+\infty} y'(x - \delta x) f(\delta x) d(\delta x)$$

where f has mean 0 and variance σ^2

Evolution system

- Suppose $S_A, S_B, r \ll 1$, we get

$$\begin{cases} \dfrac{dy_1}{dt} = f_1(y) := y_1 P_1(y) + r(y_2 y_3 - y_1 y_4) \\ \dfrac{dy_2}{dt} = f_2(y) := y_2 P_2(y) + r(y_1 y_4 - y_2 y_3) \\ \dfrac{dy_3}{dt} = f_3(y) := y_3 P_3(y) + r(y_1 y_4 - y_2 y_3) \\ \dfrac{dy_4}{dt} = f_4(y) := y_4 P_4(y) + r(y_2 y_3 - y_1 y_4) \end{cases}$$

- Change of variables $p = y_1 + y_2$ frequency of allele A, $q = y_1 + y_3$ frequency of allele B, and $D = y_1 y_4 - y_2 y_3$ linkage disequilibrium, gives

$$\begin{cases} \dfrac{dp}{dt} = 2S_A \ p(p-\alpha)(1-p) + 2S_B \ (q-\beta)D \\ \dfrac{dq}{dt} = 2S_B \ q(q-\beta)(1-q) + 2S_A \ (p-\alpha)D \\ \dfrac{dD}{dt} = -D\Big(r + 4S_A(p-\alpha)(p-\dfrac{1}{2}) + 4S_B(q-\beta)(q-\dfrac{1}{2})\Big) \end{cases}$$

with $\alpha = (S_A - s_A)/2S_A$ and $\beta = (S_B - s_B)/2S_B$.

Reaction-diffusion system

Taking migration into account

$$\partial_t y_i = f_i(y) + \partial^2_{xx} y_i$$

we get

$$\begin{cases} \partial_t p = f_1(y) + \partial^2_{xx} y_1 + f_2(y) + \partial^2_{xx} y_2 \\ \partial_t q = f_1(y) + \partial^2_{xx} y_1 + f_3(y) + \partial^2_{xx} y_3 \\ \partial_t D = y_1 f_4(y) + y_1 \partial^2_{xx} y_4 + y_4 f_1(y) + y_4 \partial^2_{xx} y_1 - y_2 f_3(y) - y_2 \partial^2_{xx} y_3 - y_3 f_2(y) - y_3 \partial^2_{xx} y_2 \end{cases}$$

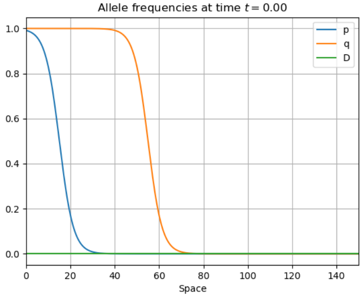
Then

$$\begin{aligned} y_1 \partial^2_{xx} y_4 + y_4 \partial^2_{xx} y_1 - y_2 \partial^2_{xx} y_3 - y_3 \partial^2_{xx} y_2 &= \partial^2_{xx} D - (2\partial_x y_1 \partial_x y_4 - 2\partial_x y_2 \partial_x y_3) \\ &= \partial^2_{xx} D + 2\partial_x p \partial_x q \end{aligned}$$

$$\begin{cases} \partial_t p = 2S_A\ p(p-\alpha)(1-p) + 2S_B\ (q-\beta)D + \partial^2_{xx} p \\ \partial_t q = 2S_B\ q(q-\beta)(1-q) + 2S_A\ (p-\alpha)D + \partial^2_{xx} q \\ \partial_t D = -D\Big(r + 4S_A(p-\alpha)(p-\frac{1}{2}) + 4S_B(q-\beta)(q-\frac{1}{2})\Big) + 2\partial_x p \partial_x q + \partial^2_{xx} D \\ p(\cdot,0) = p_0(x) \quad q(\cdot,0) = q_0(x) \quad D(\cdot,0) = 0 \end{cases} \qquad (\star_{p,q,D})$$

Simulation #1: travelling waves ?

Same direction, same speed



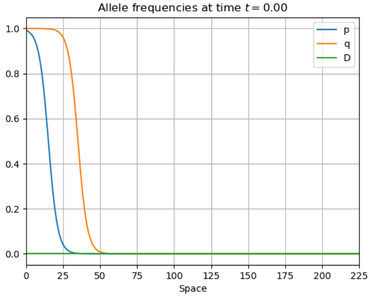
$$s_A = 0.08, \qquad S_A = 0.1, \qquad c_p = \frac{s_A}{\sqrt{S_A}} = 0.25$$

$$s_B = 0.08, \qquad S_B = 0.1, \qquad c_q = \frac{s_B}{\sqrt{S_B}} = 0.25$$

$$r = 0.01$$

Simulation #2: beware of the initial condition!

Same direction, same speed



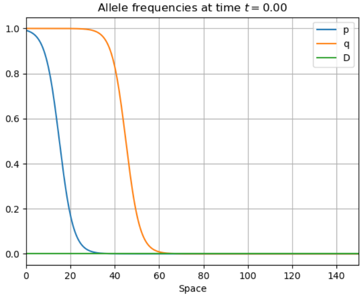
$$s_A = 0.08, \qquad S_A = 0.1, \qquad c_p = \frac{s_A}{\sqrt{S_A}} = 0.25$$

$$s_B = 0.08, \qquad S_B = 0.1, \qquad c_q = \frac{s_B}{\sqrt{S_B}} = 0.25$$

$$r = 0.01$$

Simulation #3

Same direction, speed discrepancy



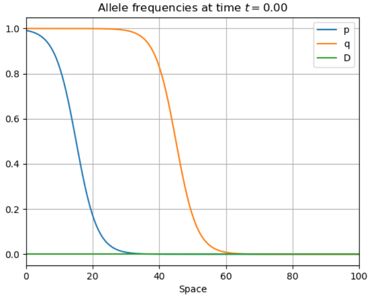
$$s_A = 0.08, \qquad S_A = 0.1, \qquad c_p = \frac{s_A}{\sqrt{S_A}} = 0.25$$

$$s_B = 0, \qquad S_B = 0.1, \qquad c_q = \frac{s_B}{\sqrt{S_B}} = 0$$

$$r = 0.01$$

Simulation #4

Same direction, (smaller) speed discrepancy

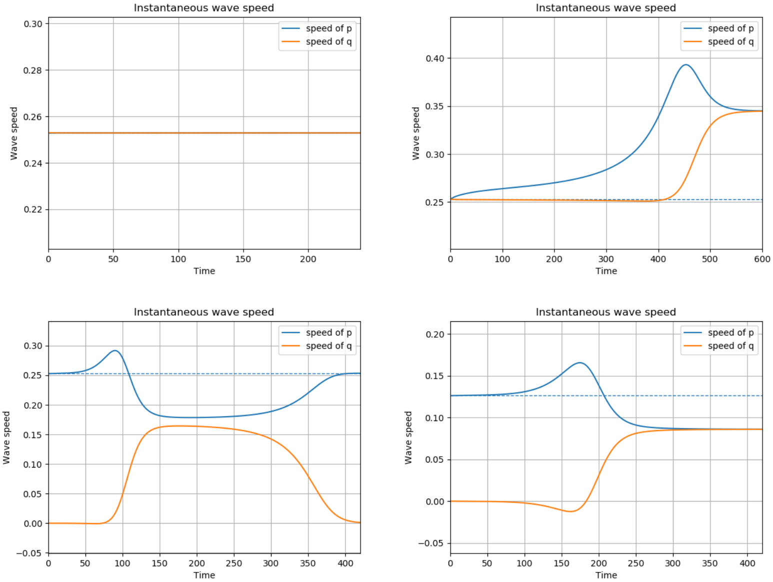


$$s_A = 0.04, \qquad S_A = 0.1, \qquad c_p = \frac{s_A}{\sqrt{S_A}} = 0.13$$

$$s_B = 0, \qquad S_B = 0.1, \qquad c_q = \frac{s_B}{\sqrt{S_B}} = 0$$

$$r = 0.01$$

Simulations: a condensed view



How are the speed computed?

- From the solutions $(p(x_n,t))_{0\leq n\leq N}$ et $(q(x_n,t))_{0\leq n\leq N}$
- Fit (at each timestep) the numerical solutions by a reference front, *i.e.* find $x_p(t)$ a minimizer of

$$\|p(x,t) - \frac{1}{1+\exp\left(\sqrt{S_A}(x-x_p(t))\right)}\|_{\ell^2}^2 = \sum_{n=0}^{N}\left(p(x_n,t) - \frac{1}{1+\exp\left(\sqrt{S_A}(x_n-x_p(t))\right)}\right)^2$$

and $x_q(t)$ a minimizer of

$$\|q(x,t) - \frac{1}{1+\exp\left(\sqrt{S_B}(x-x_q(t))\right)}\|_{\ell^2}^2 = \sum_{n=0}^{N}\left(q(x_n,t) - \frac{1}{1+\exp\left(\sqrt{S_B}(x_n-x_q(t))\right)}\right)^2$$

- Check the value of the errors for tolerance:
  $\varepsilon(x_p(t)) < 10^{-3}$ et $\varepsilon(x_q(t)) < 10^{-3}$
- Speeds are then defined by $c_p(t) = x_p'(t)$ et $c_q(t) = x_q'(t)$

Generalized travelling waves in reaction–diffusion

- Heterogeneous domain: environment, medium of propagation...

$$\partial_t p = d(x)\Delta p + f(x,p)$$

- Transition front (Berestycki, Hamel, Matano 2009):
  1. global in time solution
  2. connecting two steady states
  3. whose width remains uniformly bounded
- Generalized travelling wave (Caputo, Sarels 2011):
  1. global in time solution
  2. close to a reference front $\tilde{p}$

$$p(x,t) \approx \tilde{p}\left(\frac{x - x_0(t)}{w}\right)$$

$$p(x,t) \approx \tilde{p}\left(\frac{x - x_0(t)}{w(t)}\right)$$

- Notions of instantaneous position (and width), consequently of instantaneous speed

Generalized travelling waves in reaction–diffusion

- Heterogeneous domain: environment, medium of propagation...

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- Notions of instantaneous position (and width), consequently of instantaneous speed

Generalized travelling waves in our case study

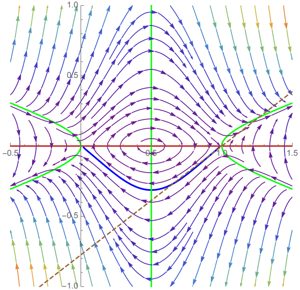
- Hypothesis on p
$$p(x,t) \approx \tilde{p}\left(\sqrt{S_A}(x - x_p(t))\right)$$
- Hypothesis on q
$$q(x,t) \approx \tilde{q}\left(\sqrt{S_B}(x - x_q(t))\right)$$
- 2 collective coordinates : x_p and x_q
- Here,
$$\tilde{p}(z) = \tilde{q}(z) = \frac{1}{1+\exp(z)} =: k(z)$$

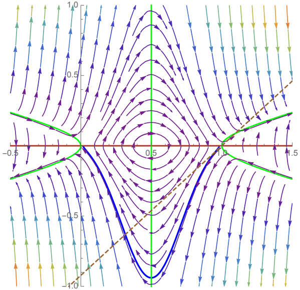
Case $S_A, S_B \ll r$: weak linkage disequilibrium

- With
$$\partial_t D \approx -Dr + 2\partial_x p \partial_x q + \partial_{xx}^2 D$$
we expect D to stay close to
$$D \approx \frac{2}{r}\partial_x p \partial_x q$$
- Because $\partial_x p$ has order of magnitude $\sqrt{S_A}$ and $\partial_x q$ has order of magnitude $\sqrt{S_B}$,
$\rightarrow$ weak linkage disequilibrium.

Case $S_A, S_B \ll r$: analytical results

- For $s = 0$, existence (and construction) of a stationary solution (standing together)
- Stability of this solution
- For $s > 0$, existence of a travelling wave solution (travelling together)

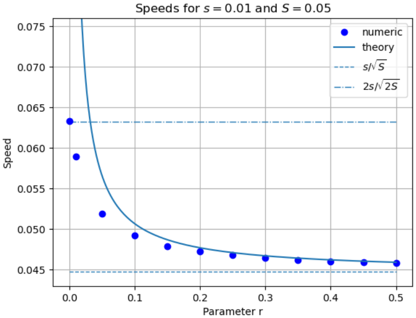




Case $S_A, S_B \ll r$: theoretical results

- Initially stacked clines *with same parameters* stay stacked
- Acceleration of the front:

$$c^* \approx \frac{s}{\sqrt{S}}\left(1 + \frac{4S}{15r}\right)$$



Case $S_A, S_B \ll r$: reduced model I

- Suppose

$$p(x,t) = k(z_p) = k\left(\sqrt{S_A}(x - x_p(t))\right) \qquad q(x,t) = k(z_q) = k\left(\sqrt{S_B}(x - x_q(t))\right)$$

we compute

$$\begin{aligned}
\partial_t p &= -\sqrt{S_A}x_p'(t)k'(z_p) & \partial_x p &= \sqrt{S_A}k'(z_p) & \partial_{xx}^2 p &= S_A k''(z_p)\\
\partial_t q &= -\sqrt{S_B}x_q'(t)k'(z_q) & \partial_x q &= \sqrt{S_B}k'(z_q) & \partial_{xx}^2 q &= S_B k''(z_q)
\end{aligned}$$

- Ansatz in the first two equations of $(\star_{p,q,D})$

$$\begin{cases}
-\sqrt{S_A}x_p'(t)k'(z_p) = 2S_A R_\alpha(k(z_p)) + \dfrac{4S_B\sqrt{S_A S_B}}{r}\Big(k(z_q) - \beta\Big)k'(z_p)k'(z_q) + S_A k''(z_p)\\
-\sqrt{S_B}x_q'(t)k'(z_q) = 2S_B R_\beta(k(z_q)) + \dfrac{4S_A\sqrt{S_A S_B}}{r}\Big(k(z_p) - \alpha\Big)k'(z_q)k'(z_p) + S_B k''(z_q)
\end{cases}$$

Case $S_A, S_B \ll r$: reduced model II

- Integrate over the spatial domain

$$\int_{-\infty}^{+\infty} k'(z)\, dz = -1, \quad \int_{-\infty}^{+\infty} k''(z)\, dz = 0, \quad \int_{-\infty}^{+\infty} R_\alpha(k(z))\, dz = \frac{1-2\alpha}{2} = \frac{s_A}{2S_A}$$

- We get the following evolution equations

$$\begin{cases} x_p'(t) = \dfrac{s_A}{\sqrt{S_A}} - \dfrac{2S_B^{1/2}(S_B - s_B)}{r} \displaystyle\int_{-\infty}^{+\infty} k'(z) k'\left(\sqrt{S_B}(x_p - x_q) + z\sqrt{\frac{S_B}{S_A}}\right) dz \\ \quad + \dfrac{4S_B^{3/2}}{r} \displaystyle\int_{-\infty}^{+\infty} k\left(\sqrt{S_B}(x_p - x_q) + z\sqrt{\frac{S_B}{S_A}}\right) k'(z) k'\left(\sqrt{S_B}(x_p - x_q) + z\sqrt{\frac{S_B}{S_A}}\right) dz \\ x_q'(t) = \dfrac{s_B}{\sqrt{S_B}} - \dfrac{2S_A^{1/2}(S_A - s_A)}{r} \displaystyle\int_{-\infty}^{+\infty} k'(z) k'\left(\sqrt{S_A}(x_q - x_p) + z\sqrt{\frac{S_A}{S_B}}\right) dz \\ \quad + \dfrac{4S_A^{3/2}}{r} \displaystyle\int_{-\infty}^{+\infty} k\left(\sqrt{S_A}(x_q - x_p) + z\sqrt{\frac{S_A}{S_B}}\right) k'(z) k'\left(\sqrt{S_A}(x_q - x_p) + z\sqrt{\frac{S_A}{S_B}}\right) dz \end{cases}$$

Case $S_A, S_B \ll r$: reduced model III

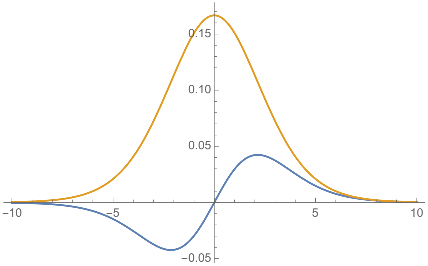
The system reads

$$\begin{cases} x_p' = c_p \quad + \dfrac{S_B}{r} f_1\left(\sqrt{S_B}(x_p - x_q), s_B\right) \\ x_q' = c_q \quad + \dfrac{S_A}{r} f_2\left(\sqrt{S_A}(x_q - x_p), s_A\right) \end{cases}$$

or

$$\theta' = c_p - c_q + F(\theta)$$

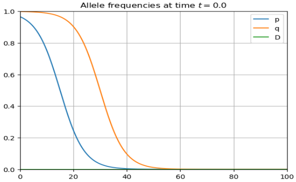
where $\theta = x_p - x_q$

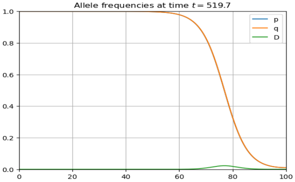


Terms f_1 in blue and f_2 in yellow

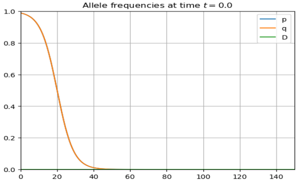
Case $S_A, S_B \ll r$: reduced model results

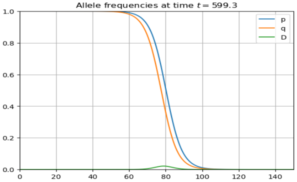
- Initially apart clines always end up stacking *or coupling*





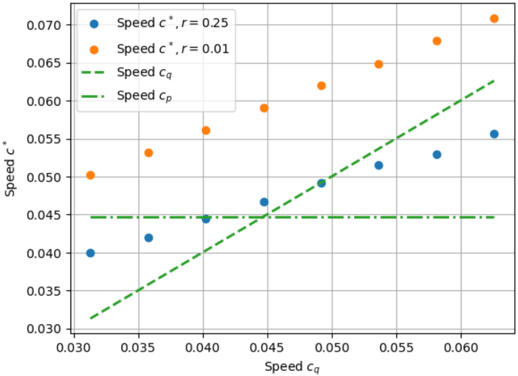
- Initially stacked clines *may start to diverge* but then end up stacked again *or coupled*





Case S_A, S_B, r arbitrary: numerical results and open questions

- Because the PDE system is more complicated, no reduced model
- According to numerical simulations:
  - More possible behaviors
  - Shift of an initially fixed cline



Population genetics equations and their solutions

Case study: two underdominant loci in diploid individuals

- Model establishment
- Numerical simulations
- Generalized travelling waves

Opening: N underdominant loci in diploid individuals

One more locus adds a layer of complexity (again!)

We rewrite $(\star_{p,q,D})$ for 3 loci first, ignoring higher order linkage disequilibrium.

$$
\begin{cases}
\partial_t p_A = 2S_A\ p_A(p_A-\alpha)(1-p_A) + 2S_B\ (p_B-\beta)D_{AB} + 2S_C\ (p_C-\gamma)D_{AC} + \partial^2_{xx}p_A \\
\partial_t p_B = 2S_B\ p_B(p_B-\beta)(1-p_B) + 2S_A\ (p_A-\alpha)D_{AB} + 2S_C\ (p_C-\gamma)D_{BC} + \partial^2_{xx}p_B \\
\partial_t p_C = 2S_C\ p_C(p_C-\alpha)(1-p_C) + 2S_A\ (p_A-\alpha)D_{AC} + 2S_B\ (p_B-\beta)D_{BC} + \partial^2_{xx}p_C \\
\partial_t D_{AB} = -D_{AB}\Big(r + 4S_A(p_A-\alpha)(p_A-\frac{1}{2}) + 4S_B(p_B-\beta)(p_B-\frac{1}{2})\Big) + 2\partial_x p_A \partial_x p_B + \partial^2_{xx}D_{AB} \\
\partial_t D_{AC} = -D_{AC}\Big(r + 4S_A(p_A-\alpha)(p_A-\frac{1}{2}) + 4S_C(p_C-\gamma)(p_C-\frac{1}{2})\Big) + 2\partial_x p_A \partial_x p_C + \partial^2_{xx}D_{AC} \\
\partial_t D_{BC} = -D_{BC}\Big(r + 4S_B(p_B-\beta)(p_B-\frac{1}{2}) + 4S_C(p_C-\gamma)(p_C-\frac{1}{2})\Big) + 2\partial_x p_B \partial_x p_C + \partial^2_{xx}D_{BC} \\
p_A(\cdot,0) = p_{A0}(x) \quad p_B(\cdot,0) = p_{B0}(x) \quad p_C(\cdot,0) = p_{C0}(x) \\
D_{AB}(\cdot,0) = 0 \quad D_{AC}(\cdot,0) = 0 \quad D_{BC}(\cdot,0) = 0
\end{cases}
$$

We then make the hypothesis of *weak linkage disequilibrium*.

3 loci, two alleles, weak linkage disequilibrium

$$\begin{cases} x'_A = c_A & + \dfrac{S_B}{r} f_{AB}\left(\sqrt{S_B}(x_A - x_B), s_B\right) + \dfrac{S_C}{r} f_{AC}\left(\sqrt{S_C}(x_A - x_C), s_C\right) \\ x'_B = c_B & + \dfrac{S_A}{r} f_{BA}\left(\sqrt{S_A}(x_B - x_A), s_A\right) + \dfrac{S_C}{r} f_{BC}\left(\sqrt{S_C}(x_B - x_C), s_C\right) \\ x'_C = c_C & + \dfrac{S_A}{r} f_{CA}\left(\sqrt{S_A}(x_C - x_A), s_A\right) + \dfrac{S_B}{r} f_{CB}\left(\sqrt{S_C}(x_C - x_B), s_B\right) \end{cases}$$

- More intricate than for 2 loci
- Theoretically harder
- Numerical simulations

The case of N genes and the connection with the Kuramoto model

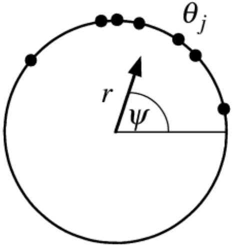
With N loci, at first order approximation, if $s_{A_i} = s_i$ and $S_{A_i} = S$, we get

$$x_i' = c_i + \frac{S}{r}\sum_{j=1}^{N} f_1(x_j - x_i, s_j) + \frac{1}{r}\sum_{j=1, j\neq i}^{N} f_2(x_j - x_i, s_j), \quad i \in \{1, \dots, N\}$$

- (Strong) similarity with the Kuramoto model

$$\theta_i' = \omega_i + \frac{K}{N}\sum_{j=1}^{N} \sin(\theta_j - \theta_i), \quad i \in \{1, \dots, N\}$$

- Differences : phase space, normalization constant $1/N$



$re^{i\psi} = \frac{1}{N}\sum e^{i\theta_j}$

Conclusion

- Interacting genetic incompabilities
- Theorems are possible in some restrictive situations
- Generalized travelling waves allow to go a step further
  1. Numerically
  2. Conceptually
- System of N clines $\rightarrow$ system of N points!

Thank you for your attention!

Conclusion

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Thank you for your attention!